

IV. *Cyrtoctenus* gen. nov., a large late Palaeozoic Arthropod with pectinate Appendages.*
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SYNOPSIS

It is confirmed that the type species of the genus *Glyptoscorpius* Peach 1882 is a subjective synonym of *Adelophthalmus* Jordan and Meyer 1854. Species which have been referred to *Glyptoscorpius* are reviewed and their present taxonomic position defined. *Cyrtoctenus* gen. nov., type species *Cyrtoctenus peachi* sp. nov., is designated to accommodate forms bearing five pairs of specialised abdominal appendages of which the first is comb-like. Four species of *Cyrtoctenus* from Devonian and Carboniferous rocks in Scotland, England, Belgium and Czechoslovakia are recognized. The structure and affinities of these forms are discussed with special reference to the comb-like appendages and their ornamentation in relation to these features in other arthropods. In particular the development of filaments and fulcra from different types of scales is discussed. The characters of the new genus are found to be so distinctive as to require the creation of the new order CyrtocTENIDA for its accommodation.

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I. INTRODUCTION

THE genus *Glyptoscorpius* was erected by B. N. Peach (1882) who defined it as comprising "Segmented animals with horny integuments sculptured as in *Eurypterus*, composed of carapace with sub-central simple eyes, and twelve other body segments, and provided with comb-like appendages as in scorpion, the walking legs having bi-ungulate tips". No type species was designated by Peach but *G. perornatus* Peach was the first species described under the generic name and was designated the type species by Diener (1924), see also Kjellesvig-Waering (1948), Størmer (1955) and Waterston (1957). The species is known from a unique holotype from the Lower Carboniferous of the River Esk at Glencartholm, 3½ miles S.S.E. of Langholm, Dumfriesshire. Peach (1882) recognised the specimen, previously described as a plant under the name *Cycadites caledonicus* by J. W. Salter (1863, 1866), which had been found in the Lower Carboniferous Cove-Cockburnspath section of East Lothian, as belonging to his new arthropod genus. He also referred a number of specimens and *dissecta membra* from Langholm and Tarras Waterfoot in Eskdale, the Tweeden Burn in Liddesdale and Lennel Braes in Berwickshire to *Glyptoscorpius*. He later recognised *G. caledonicus* in material collected by J. Rhodes in the Coomsdon Burn, ½ mile above its junction

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with the River Rede in Northumberland and in the memoir dealing with that district (Peach 1887a) *Glyptoscorpium argus* Peach M. S. and *Glyptoscorpium* sp. are also recorded from the Coomdsdon locality. Peach (1887b) described *G. minutisculptus* from the Coal Measures of Mount Vernon, Glasgow and in the following year *G. kidstoni* from the Upper Carboniferous (Radstockian) at Radstock, Somerset (Peach 1888).

In the subsequent literature much confusion exists about Peach's genus. It is clear that some of the characters claimed for the genus in the original diagnosis are either questionable or without meaning. For example the posterior end only of the head shield of the unique holotype of *G. perornatus* is known, and the prosoma of *G. caledonicus* is unknown, and since the diagnosis was based on these two species there can be no evidence to support Peach's claim that the carapace has sub-central simple eyes, except perhaps his own guess in the description of *G. caledonicus* "Carapace unknown. It was probably semicircular, with sub-central simple eyes like those of *Eurypterus Scouleri* Hibbert." The presence of bi-ungulate tips to the walking legs is another character which later work suggests must be questioned. Peach (1882, figs. 11, 11a) described and figured the distal extremities of two detached limbs which he regarded as belonging to *Glyptoscorpium* since they were found in association with material belonging to that genus from Glencartholm and Lennel Braes. It has been shown by one of us (Størmer, 1963, pp. 48–51), however, that it is more probable that the Glencartholm specimen G.S.E. 2174 (Peach 1882, fig. 11) belongs to *Gigantoscrapio willsi* Størmer, a large scorpion which occurs in the same beds at that locality.

Because of confusion caused by the fragmentary nature of the material, the unsatisfactory definition of the genus *Glyptoscorpium* and by the fact that the type species of that genus is now considered referable to the more common genus *Adelophthalmus*, a review of species which have formerly been included in *Glyptoscorpium*, together with others possessing similar comb-like appendages but which have been included in other genera, is overdue. A re-examination of the minute structures of these comb-like appendages is also desirable because they demonstrate morphological features which are of interest in considering the evolution of the arthropods. The present work has been concerned with a re-examination of these problems, and, in so far as the limited nature of the available material will allow, the anatomy of the comb-like organs and associated appendages is described and their phylogenetic significance discussed.

In the descriptions, material from the British Museum (Nat. Hist.) bears the prefix B.M.(N.H.) before the registered numbers quoted, while those from the Institute of Geological Sciences in London are prefixed G.S.M., from the Leeds office G.S.(L.) and from the Scottish office G.S.E. Specimens from the University of Liège have the prefix R.E.

II. THE STATUS OF FORMS REFERRED TO *Glyptoscorpium* PEACH

Over forty years ago W. A. Bell (1922, p. 165) recognised *G. kidstoni* Peach as belonging to the Carboniferous eurypterid genus *Adelophthalmus* (*Anthraconectes auct.*), a determination supported by Kjellesvig-Waering (1948, p. 7). The unique holotype of *G. perornatus* Peach was re-examined by one of us (Waterston 1957, p. 266) who confirmed the lack of comb-bearing appendages or bi-ungulate walking legs in the specimen, the ornamentation, size and proportions of which (Pl. VI, figs. 1, 2) make the specimen referable to *Adelophthalmus*. Since this species is the type species of *Glyptoscorpium* (Diener 1924) Peach's genus must therefore become a subjective synonym of *Adelophthalmus*. The Upper Carboniferous form *G. minutisculptus* Peach was also recognised as an eurypterid by Waterston

(1957, p. 283) who has recently designated it the type species of the new genus *Vernonopterus* (Waterston 1968).

In the present paper the type specimen of *G. caledonicus* (Salter), from the Cove-Cockburnspath section of Berwickshire, is found to be specifically distinct from the comb-bearing forms found in other parts of southern Scotland and Northern England which were included in it by Peach (1882, 1887a). For these the new species *Cyrtoctenus peachi* is here described and chosen as the type species of the new genus *Cyrtoctenus*. The new genus is erected to embrace the comb-bearing species now no longer referable to *Glyptoscorpius* and includes *C. caledonicus* (Salter) as here emended.

The present status of species previously referred to *Glyptoscorpius* is:

Glyptoscorpius argus Peach 1887a = *Nomen nudum*.

Glyptoscorpius caledonicus (Salter) Peach 1882, 1887a =

partim *Cyrtoctenus caledonicus* (Salter) emend

partim *Cyrtoctenus peachi* sp. nov.

Glyptoscorpius kidstoni Peach 1888 = *Adelophthalmus kidstoni* (Peach)

Glyptoscorpius minutisculptus Peach 1887b = *Vernonopterus minutisculptus* (Peach)

Glyptoscorpius perornatus Peach 1882 = *Adelophthalmus perornatus* (Peach)

Glyptoscorpius stevensoni (R. Eth. jun.) Anderson 1936 = *Dunsopterus stevensoni* (R. Eth. jun.)

III. PALAEOONTOLOGICAL DESCRIPTIONS

Genus *Cyrtoctenus* gen. nov.

Diagnosis.—Arthropod bearing a series of probably five, abdominal, elongate, unjointed appendages, each probably borne on a basal segment. The first appendage (A) is characterised by its comb-like form and consists of a curved rachis or shaft tapering gradually towards the distal end, ornamented with elongate tongue-shaped scale-tubercles, and bearing on its posterior concave margin two rows of long narrow flat filaments. The second appendage (B) tapers distally, is curved, ornamented with tongue-shaped scale-tubercles on one side and "eurypterid" scales on the other, and its concave posterior border bears one row of dagger-shaped fulcra on one side, and one intra-marginal row of moderately short, narrow flat filaments on the other side. The third appendage (C) resembles the second appendage (B), but differs in having large "eurypterid" scales near the anterior border. The fourth appendage (D) resembles the second appendage (B), but differs in having large "eurypterid" scales along the posterior border and less developed fulcra. Another, probably fifth appendage (E) has a straighter rachis ornamented with elongate "eurypterid" scales or flat tubercles, and bearing at its posterior convex margin one row of distally dagger-shaped fulcra, no intra-marginal filaments are present on the other side. The filaments on the first and second appendages are devoid of peg organs characteristic of scorpionid combs.

Type species: *Cyrtoctenus peachi* gen. et sp. nov.

Derivatio nominis: Greek, *Cyrtoctenos*: a curved comb.

The following species are recognised as belonging to the genus in addition to the type species: *Glyptoscorpius caledonicus* (Salter), *Eurypterus dewalquei* Fraipont and *Stylonurus* (*Ctenopterus*) *ostraviensis* Augusta and Přibyl.

(a) *Cyrtoctenus peachi* sp. nov.

Pl. I, figs. 5–17; Pl. II, figs. 1–2, 7–18; Pl. III, figs. 1–16, 17?, 18?; Pl. V, figs. 1–11;
Pl. VI, figs. 3–13; Text-figs. 1–8, 9?, 10, 13.

Glyptoscorpis caledonicus Peach partim. Peach 1882, pp. 618–525, Pl. 28, figs. 14, 15?, Pl. 29, figs. 17, 20–22. Peach in Miller 1887a, p. 84.

Glyptoscorpis argus Peach M. S. in Miller 1887a, p. 84.

Holotype.—Specimen contained in three pieces G.S.E. 2184–2186 from the Calciferous Sandstone Measures of Lennel Braes, Tweedmill, near Coldstream, Berwickshire.

Derivatio nominis.—named after Benjamin Neave Peach (1842–1926) who first brought this material before the scientific public.

Material.—The more important specimens upon which the description has been based are:

- (a) Lennel Braes, Tweedmill, near Coldstream, Berwickshire, G.S.E. 2184–2186 (holotype), G.S.E. 2127, G.S.E. 9682, G.S.E. 2144.
- (b) Coldstream Bridge, Coldstream, Berwickshire, G.S.E. 2183, G.S.E. 5864.
- (c) Crooked Burn, Foulden, Berwickshire, B.M. (N.H.) In 25982.
- (d) “Tarras Waterfoot, Eskdale, Dumfriesshire”, G.S.E. 9683/9684.
- (e) Glencartholm, Eskdale, Dumfriesshire, G.S.E. 2180?
- (f) Coomsdon Burn, Redesdale, Northumberland, G.S. (L) R.1729, G.S.(L) 1733, G.S.(L) R.1573.
- (g) Longcraig Bay, East of Belhaven Bay, Dunbar, East Lothian, G.S.E. 12298.

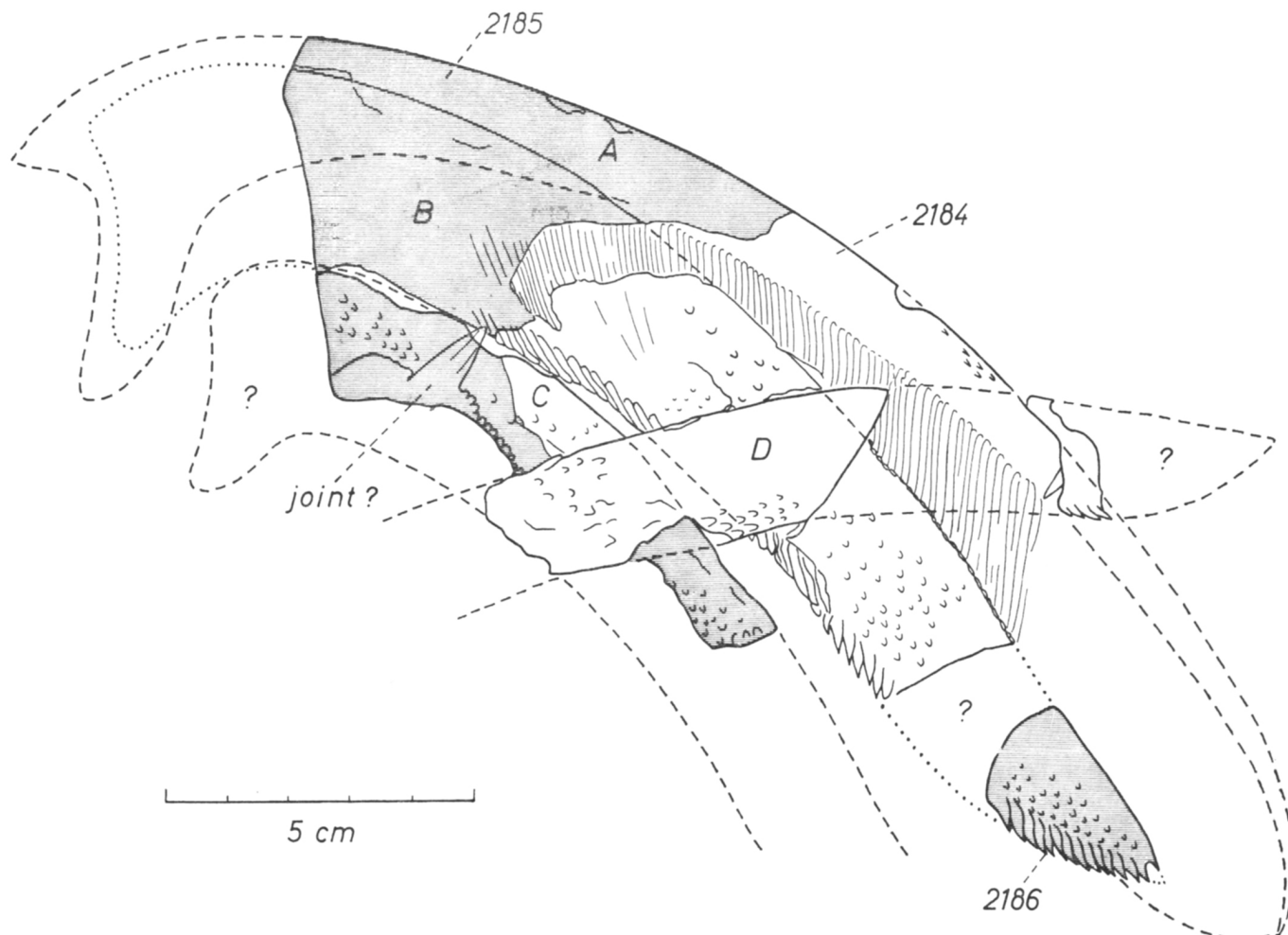
Diagnosis.—Cyrtoctenid in which appendage (A) has a large number of filaments and appendage (B) moderately long filaments and large fulcra.

Description:

Appendage A.—The scythe-shaped, unjointed rachis or shaft, of which the greatest observed length is that of the holotype which when complete must have been 240 mm., tapers gradually towards the distal point and was apparently dorso-ventrally flattened (Pl. I, figs. 6, 7; Pl. V, fig. 5; Text-figs. 1–3). The distal portion of the shaft becomes very narrow thus resembling the distal filaments (Pl. III, fig. 2; Text-fig 3a). The shaft is attached by a joint to a small subrectangular basal plate and there are indications that this plate is attached to the ventral body wall through an interposed article (Pl. III, fig. 1; Text-fig. 2). The proximal posterior margin of the shaft is concave, and near the base is produced to form a tongue-shaped posterior process which abuts on the basal plate and which may have slid across it when the appendage was moved backwards. There are indications of the presence of a longitudinal ridge on the ventral side of the shaft in the proximal part, which here parallels the posterior margin of the rachis.

Both sides of the shaft have a characteristic ornamentation which consists of elongate scale-tubercles having their long axes parallel to the anterior margin and pointing distally. Along and near the anterior margin tubercles may be rather large with a length of 1–3 mm. and a maximum width of 0.4 mm., further back they become smaller and less conspicuous, the width being only 0.1–0.15 mm. (Pl. I, fig. 5; Pl. III, fig. 3; Text-figs, 3, a, b; 13). The smaller scale-tubercles may only have the distal, elevated part distinguished, giving the impression of short scales (Pl. I, fig. 5). The protruding scale-tubercles (particularly well seen in G.S.E. 2183, Pl. III, figs. 2,3) represent a thickening of the cuticula and are not assoc-

iated with a corresponding invagination of the lower surface. The dark skin of the tubercles is indicated in the slides on Plate I, figs. 9–11. A particular elaboration of the scale tubercles may occur along the anterior margin in the distal portion of the rachis (e.g. in G.S.E. 2183, Pl. III, fig. 2; Pl. VI, fig. 7; Text-fig. 3a). Here the scale tubercles are modified to form flat, partly overlapping spines directed distally and forming an angle of about 20° with the direction of the anterior margin of the rachis. Each flat spine, the largest one measuring 5 mm. in

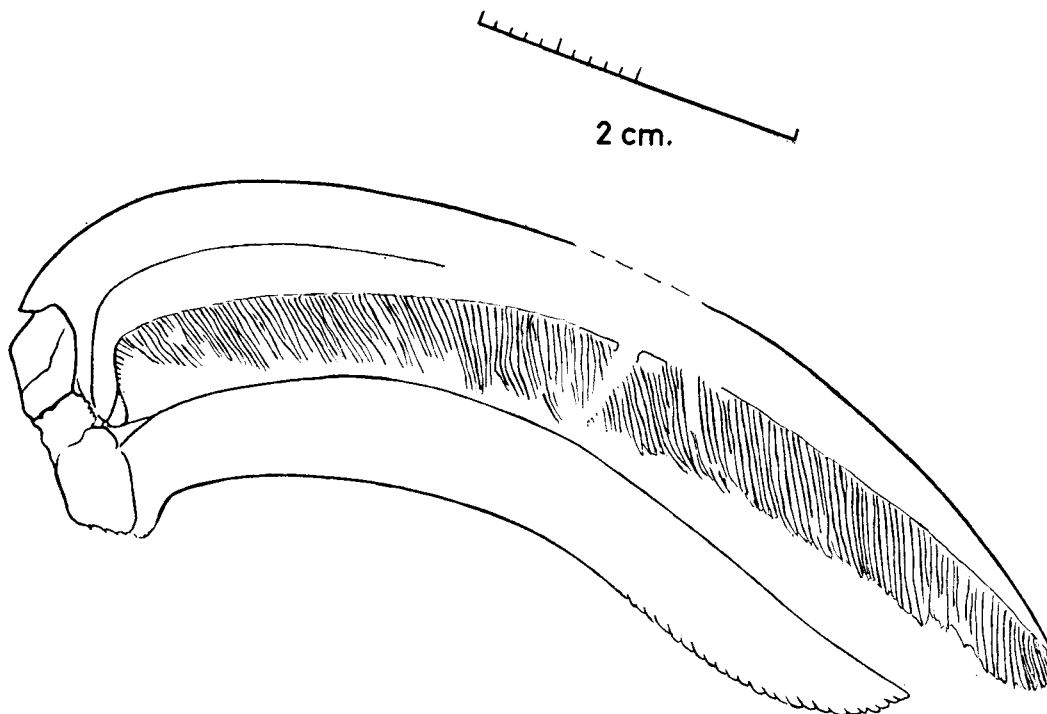


TEXT-FIG. 1.—Diagram of holotype of *Cyrtoctenus peachi* n.g. n.sp. The three specimens G.S.E. 2184, 2185 and 2186 are combined in one figure. The serrated margin of a joint (segment) of a possible prosomal appendage is indicated in the shaded specimen G.S.E. 2185.

length and 0.5 mm. in width, tapers gradually in width towards the point. They resemble somewhat the filaments at the posterior margin. The largest spines occur 20–40 mm. from the tip of the shaft in G.S.E. 2183. 10–20 mm. from the tip the spines are quite short, and on the distal 10 mm. the margin is smooth.

Two rows of long flat filaments are borne on the concave posterior border of the rachis. In one complete specimen (G.S.E. 2127, Pl. II, fig. 18) about 170 filaments occur in each row along a shaft 65 mm. in length. The filaments have their long axes set at an angle of from 30° to 70° to the axis of the rachis (Text-fig. 3a, b). These angles may vary through the length of the rachis and from one row to the other, suggesting that the filaments were flexible to a considerable extent. Their flexibility is also indicated by twisting (Pl. II, fig. 17, left;

Pl. VI, fig. 5, Text-fig. 3f) and the overlapping of the filaments (Pl. III, figs. 2, 7). Throughout their length the filaments are fairly straight except for an outward curve towards their posterior end. The blades of the filaments in the two rows are attached to the rachis *en echelon*, the filaments overlapping each other towards the distal end of the rachis, each being overlapped by its proximal neighbour. In posterior view (right angle to plane) the angle between the filaments is 20–25 degrees (Text-fig. 3e). The length of the filaments is about three times the breadth of the rachis becoming more towards the distal end of the rachis. Each filament is blade-shaped with nearly flat surfaces, the width of the filaments in larger specimens is



TEST-FIG. 2.—Appendages A and B of a smaller specimen of *Cyrtoctenus peachi* n.g. n.sp. G.S.E. 2127.

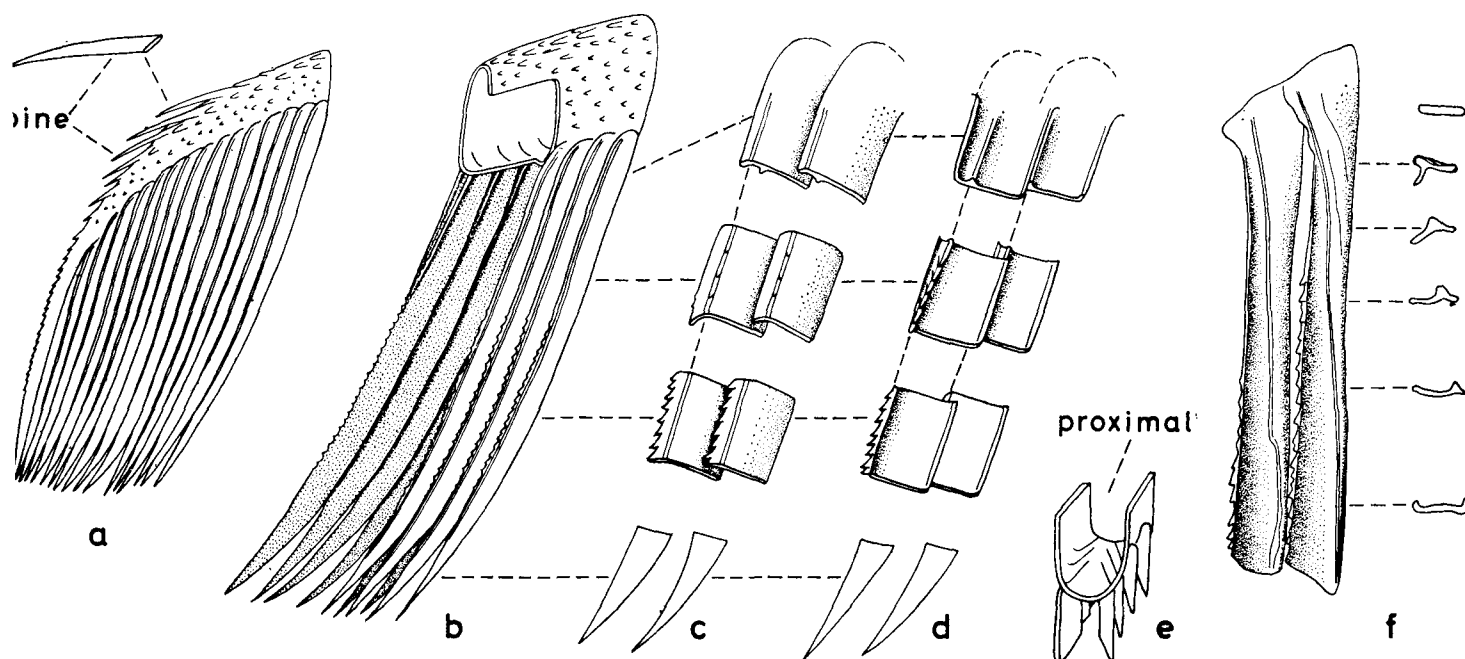
1.0–1.1 mm., the thickness only 0.05 mm., but they sometimes become a little thicker towards the margins. The inner surfaces of the filaments of each row, which are opposed to one another, are flat or slightly concave. The outer surfaces, that is the dorsal surfaces of the dorsal row of filaments and the ventral surfaces of the ventral row, are flat or slightly convex with a narrow ridge developed near the margin facing the distal point of the rachis. This longitudinal ridge is not distinct near the base of the filament (Pl. III, fig. 8), and is intra-marginal further out (Pl. III, fig. 9; Text-fig. 3c). It may be continuous or consist of elongate drop-like tubercles (Pl. III, fig. 10) directed towards the tip of the filament. The surface of the filament outside the ridge may be bent inwards (Pl. III, fig. 9, middle; Text-fig. 3c). A marginal or intra-marginal row of denticles occurs on the ridged or distal side of the filament (Pl. III, figs. 9, 10, 12, 14–16; Text-fig. 3b–d, f). The position of the row of denticles varies from specimen to specimen and on the filament itself. A marginal position is common (Pl. III, figs. 9, 10), but the row of denticles often migrates to the inner surface of the filament (Pl. III, figs. 14–16; Text-fig. 3d). This position occurs near the base of the filament.

Peg organs, characteristic of true scorpions, have not been found on the filaments, microscopic preparations from G.S.E. 2127 showing only a few small randomly distributed circular light spots.

Appendage B.—The unjointed, flattened, rachis of appendage B, as in appendage A, is attached to a basal plate which is shorter than that of appendage A against which it abuts (seen in G.S.E. 2127, Pl. III, fig. 1; Text-fig. 2).

The anterior border of the finger-shaped rachis is curved (convex) in the proximal part

App. A

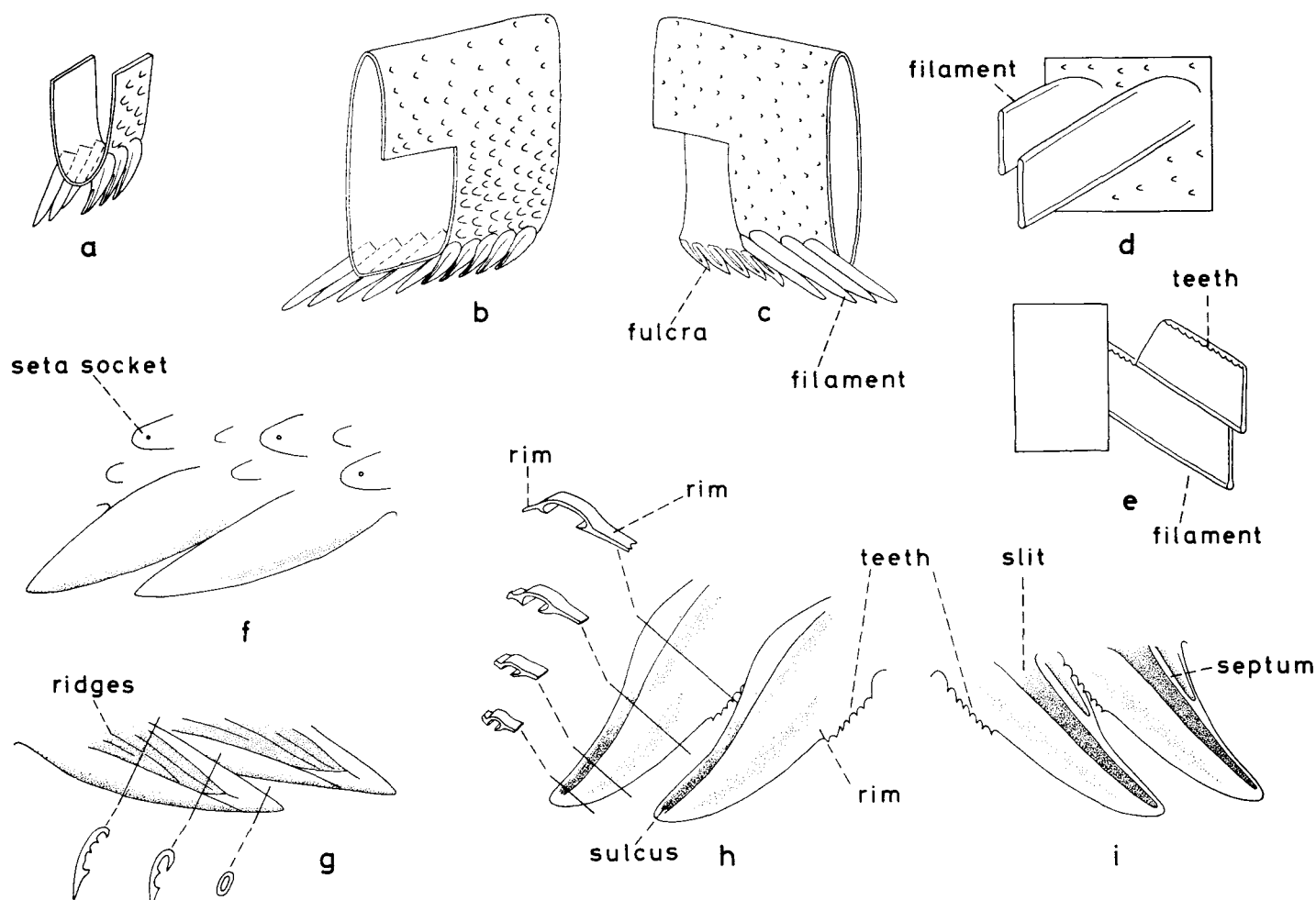


TEXT-FIG. 3.—Appendage A of *Cyrtoctenus peachi* n.g. n.sp. Diagrams showing various parts and details of the appendage. *a.* tip of appendage; *b.* rachis with the two rows of filaments (one row shaded); *c.* *d.* outer and inner surface of filaments; *e.* diagram indicating position of filaments in relation to shaft; *f.* twisted filaments shown in Pl. VI, fig. 3.

and straight to slightly concave in the distal part. The width of the rachis tapers in the distal part, as is well seen in G.S.E. 12298 (Pl. VI, fig. 3). A proximal tongue-shaped process or “lade” is indicated in specimen G.S.E. 2127 (Pl. III, fig. 1; Text-fig. 2), a structure similar to, but shorter than, the equivalent process in appendage A. The estimated length of the longest type B rachis seen, that of the holotype, is about 200 mm. The rachis has a distinct ornamentation except in the most proximal portion where the skin is fairly smooth. The ventral surface of the rachis has parabolic scales of eurypterid type closing distally in a steep margin (Pl. I, figs. 12, 16, 17; Pl. VI, fig. 6; Text-figs. 4*b*, *f*; 5). The size of the scales varies, a width ranging from 0.5–0.8 mm. being common in the holotype. In the proximal portion of the rachis the scales are less conspicuous, while distally (Pl. II, fig. 7) the scales are smaller and more elongate. The scales are orientated distally except near the posterior margin of the rachis where they are directed slightly more posteriorly (Pl. I, figs. 16, 17; Pl. II, fig. 7). Some of the scales have a circular perforation, evidently a seta socket (Pl. VI, fig. 6). Text-fig. 5 shows a slide of the scales in a smaller specimen (G.S.E. 2127). At the posterior border the scales develop into fulcra, which, however, are chiefly confined to the distal half of the rachis. The intricate structure of the dagger-shaped fulcra may be understood by following

the development of the appendage in the holotype from the proximal to the distal portion of the rachis. The location of the structures described below refers to the specimen illustrated in Text-fig. 2.

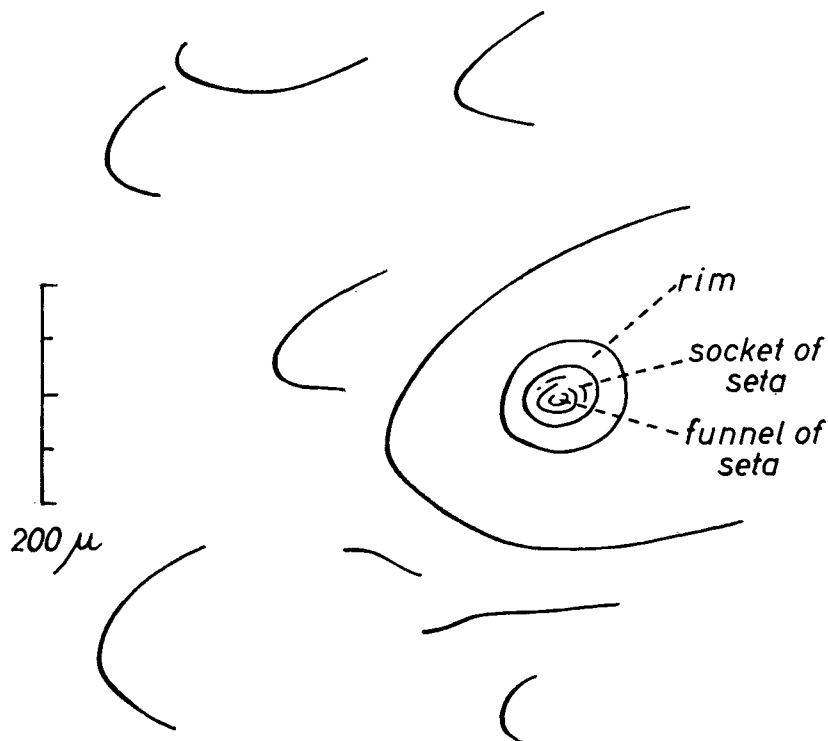
App. B



TEXT-FIG. 4.—Appendage B of *Cyrtoctenus peachi* n.g. n. sp. Diagrams showing various parts and details of the appendage. a. position of filaments and fulcra in relation to rachis; b, c. ventral and dorsal view of rachis with filaments and fulcra; d. attachment of filaments some distance from the margin; e. the same in dorsal view showing denticles on filaments; f, g. ventral and dorsal view of the fulcra about midway on the appendage; h, i. ventral and dorsal view of the fulcra near the tip of the appendage.

The proximal portion of the rachis, 160 mm. from the tip, has but little ornamentation and the posterior border has no protruding scales, only an indication of a thickening of the wall along the posterior border. At 150 mm. there are still no protruding scales, only the outline of long scales parallel to the border. At 100 mm. the parabolic scales are distinct, and the posterior border of the rachis is covered by scales bent around so that one part of the scales occurs on the dorsal and one on the ventral surface (Text-fig. 13h). At 80–72 mm. the fulcra develop rather suddenly. The tips of the scales bent around the border of the rachis protrude more and more forming short fulcra. To begin with they are well separated,

but gradually they become more prolonged and partly overlap each other (Text-fig. 13*i*). The scales or fulcra at the edge have a thickness of the integument of about 0.1 mm., *i.e.* considerably thicker than the scales elsewhere on the rachis. At 70 mm. from the tip elaborate fulcra develop. A preparation was made in which part of the skin, including the posterior border with fulcra and filaments, was removed to show both the ventral and dorsal surfaces (Pl. I, figs, 12, 13; Text-fig. 4*f, g*). Pl. I, figs, 16, 17 show the appendage before and after the removal of the piece. The fulcra obviously develop from parabolic scales at the margin. In the typical fulcra, however, the tips of the scales are considerably prolonged in a postero-distal direction forming an angle of 20°–40° with the direction of the rachis.



TEXT-FIG. 5.—Scales on the ventral surface near the posterior margin of the rachis of appendage B in *Cyrtoctenus peachi* n.g. n. sp. G.S.E. 2127/1.

The fulcra are asymmetrical. The primary distal opening or slit between the ventral and dorsal parts of the bent marginal scale is situated on the dorsal side (Text-fig. 4*g*). This indicates that the main part of the original scale remained on the ventral side and only a smaller part on the dorsal side. The distal slit seems to continue almost to the tip of the fulcrum (Pl. I, fig. 13; Text-fig. 4*g*). Inside the fulcrum (Pl. I, fig. 13) the surface has several ridges, longitudinal or oblique (Text-fig. 4*g*). These ridges might have served to strengthen the fulcrum. Towards the tip of the appendage from a distance of 55 mm. from it (Pl. II, figs. 7–10), the fulcra become even more specialised. These fulcra are narrowly triangular in form having a convex proximal and a concave distal margin. They partly overlap one another so that the basal part of the distal margin is partly concealed in ventral view (Pl. II, fig. 10). The bases of the fulcra are not well defined, the fulcral margins continuing on the rachis as ridges similar to, and having the same direction as the lateral borders of the scales on the rachis. The distal slit of the fulcrum is dorsal (Pl. II, fig. 9; Text-fig. 4*i*); on the ventral surface a spoon-like furrow or sulcus occurs near the tip (Pl. II, fig. 8; Text-fig. 4*h*). On the ventral surface of the fulcrum longitudinal ridges and shallow grooves may appear

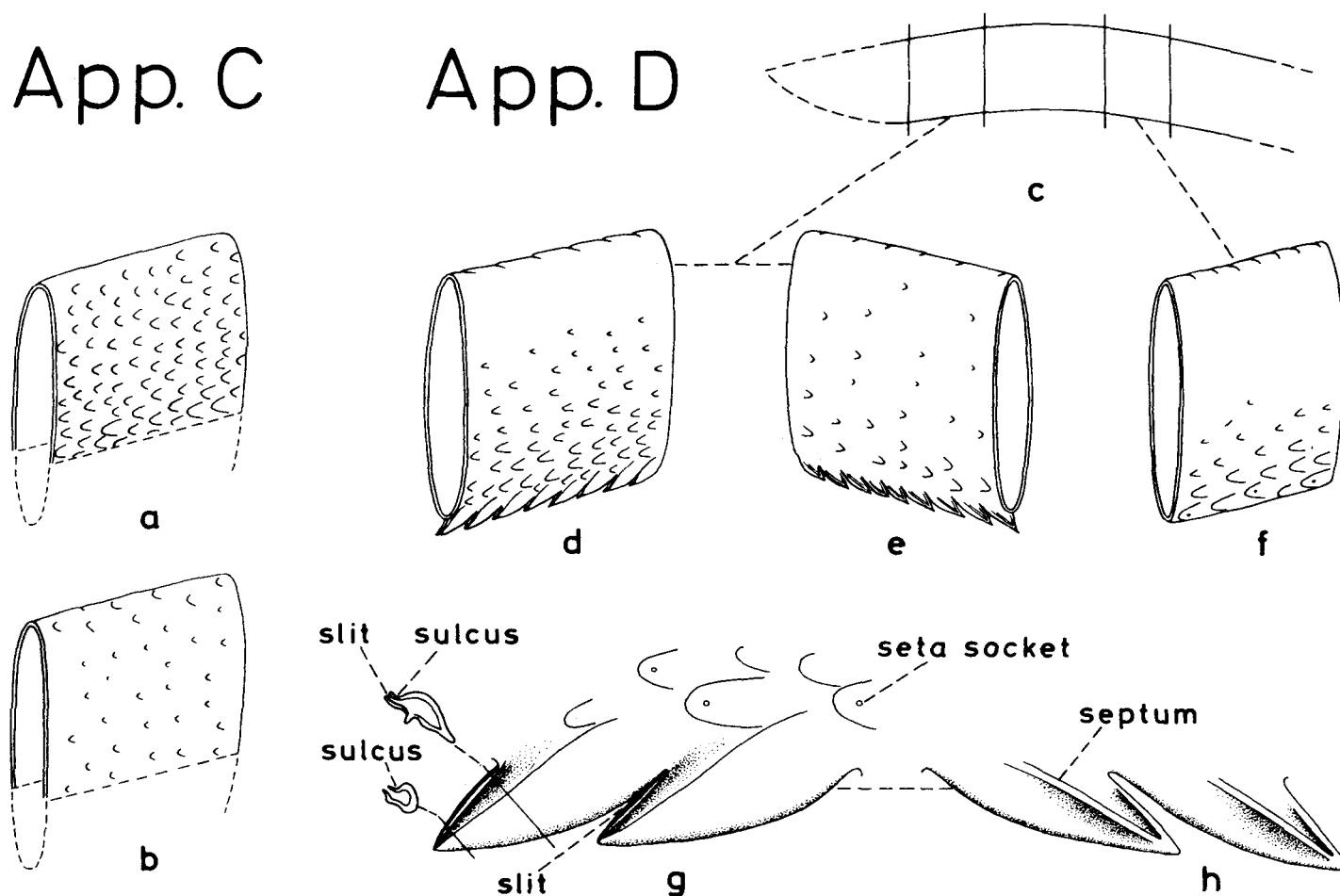
(Pl. II, figs. 7, 10). Where the ventral skin is broken off various ventral and lateral walls or septa may be recognised (Text-fig. 4i). A broad and flat rim develops on the proximal side of the fulcrum (Text-fig. 4h). The rim probably represents an outgrowth of the skin at the original bend of the scale. Near the base of the fulcrum the rim is provided with 6–7 spines, the length and distance between them being 0.2 mm. (Pl. II, fig. 10). On the distal side of the fulcrum another, narrower rim develops. This usually has a more dorsal direction (Text-fig. 4h).

The dorsal surface of the rachis has a different ornamentation and near its posterior border is provided with filaments instead of fulcra. In the proximal part, about 105 mm. from the tip (Text-fig. 1), the skin is practically devoid of tubercles or scales. Near the anterior margin traces of a few scattered elongate scales may seem to be orientated opposite to normal, *i.e.* directed proximally, but this is probably due to a more or less elliptical outline of some of the elongate scales. At 100 mm. a few scattered scale-tubercles are present. They are short, triangular in shape, and the raised distal part has a nearly vertical distal wall. The width of the scales is 0.3 mm. and the length of the raised part 0.2 mm. About 75 mm. from the distal end of the appendage, the triangular scales become more parabolic and their tips more rounded (Pl. V, fig. 4). The moderately raised part is well marked while the base is rather indistinct. A few of these scattered scales also occur near the posterior margin, posterior to the filaments. At 65 mm. the scales near the anterior margin (only a few preserved) appear to be tongue-shaped with a width of 0.2–0.3 mm. and a length of about 0.7 mm.

Characteristic of the dorsal surface are the filaments attached in a row not far from the posterior margin of the shaft and reaching as far as the tips of the fulcra (Pl. I, figs. 6, 8, 12–15, 17; Pl. V, figs. 2–4; Text-figs. 4a–e). The filaments do not seem to be present on the proximal $\frac{1}{3}$ – $\frac{1}{4}$ of the rachis. While the fulcra occur close to the posterior margin, the filaments are intra-marginal, attached about 3.3 mm. from the border (Pl. I, fig. 6; Text-fig. 4d). The removed piece, described above (Pl. I, fig. 13) shows the position of the filaments in relation to the fulcra on the ventral side. The filaments have more or less the same orientation as the fulcra below (Text-fig. 4b, c), and they form a somewhat smaller angle 20°–30°, with the long axis of the rachis, the smallest angle occurring in the proximal part of the shaft (Pl. I, fig. 6). The filaments are attached *en echelon* and, like the fulcra, overlap each other towards the tip of the appendage (Pl. I, fig. 8; Pl. V, fig. 4; Text-figs. 4a, c, d). As in appendage A, the overlapping fulcra are blade-shaped but they lack the ridge on the outer, ventral surface. They are slightly broader than in appendage A, having a width at the base of 1.5 mm. and a length up to 12 mm. Instead of slowly tapering along their length, such as in appendage A, the filaments tend to be rather blunt (Pl. I, figs. 15 and 17). In some of the filaments an intra-marginal row of short denticles is indicated on the dorsal side, similar to conditions in appendage A (Pl. V, figs. 2 and 3; Text-fig. 4e). The flat or slightly concavo-convex filaments have faint indications of marginal thickening as seen in Pl. I, figs. 13 and 14, and Pl. V, figs. 2–4.

Appendage C.—Only the anterior half of the rachis of this appendage is preserved in the holotype having a length of 85 mm. (Pl. I, fig. 6; Pl. II, fig. 1; Pl. V, fig. 1; Text-figs. 6a, b). The distal portion of the probably finger-shaped appendage is lacking. Although the skin is much crumbled, the ornamentation on the ventral surface is well preserved, but only smaller parts of the dorsal skin are preserved. The ventral surface is covered by distinct eurypterid scales with parabolic to elliptical outline and directed distally (Pl. II, fig. 1). The largest scales measure 2.1 mm. in width and about 2.0 mm. in length. Smaller scales with a width about 0.5 mm. and a length of 1.0 mm. are common. The scales become less distinct

towards the anterior margin of the rachis. The dorsal surface has only small and very scattered scales of a triangular outline, similar to those occurring on both the dorsal and ventral surface of appendage A, and on the dorsal surface of appendage B. The scales may be regarded as tongue-shaped scale-tubercles in which the elongate proximal portion has become obsolete. Just at the anterior margin a few larger sigmoid scales occur, measuring 1.0 mm. in length with a width of 0.4 mm.



TEXT-FIG. 6.—Appendages C and D of *Cyrtoctenus peachi* n.g. n.sp. Diagrams showing structure of rachis and fulcrum. *a, b.* ventral and dorsal surface of the little-known appendage C; *c.* outline of rachis of appendage D to show the position of diagrams *d, e, f*; *d, e.* ventral and dorsal surface of rachis with filaments; *f.* ventral surface; *g, h.* ventral and dorsal surface of fulcrum in distal part of appendage.

Appendage D.—The crossing appendage in the holotype (Pl. I, fig. 7; Pl. II, fig. 2; Pl. V, figs. 5, 8–10; Pl. VI, figs. 6, 7; Text-fig. 1) apparently represents a fourth appendage. At first we thought the appendage to be the other dislocated appendage C, but the ornamentation proved to be different. 100 mm. of the finger-shaped, slightly curved appendage is preserved. The width of the rachis is 20 mm., a little less than a width of 25 mm. in appendage B. The part of the fringe of filaments obscuring appendage D in Pl. V, fig. 5 has been removed exposing more of the rachis and the fulcrum along the posterior margin (Pl. VI, fig. 9).

The proximal portion of the rachis is rather smooth without scales. At the anterior margin, 10 mm. from the left border of the preserved portion of the specimen three flat and blunt spines occur (Pl. VI, fig. 8). They are directed distally, forming an angle of 20°–30°

with the main axis of the rachis. The free part of the 1.1–1.2 mm. wide spines is 3.0 mm. long but the borders continue about 3.0 mm. on the dorsal side of the rachis. Distally large scales gradually appear near the posterior border of the rachis. At a distance of 40 mm. from where the rachis is broken off, the scales are paraboloid to subtriangular in outline with a width up to 1.5 mm.; the length is difficult to measure since the borders of the scales become gradually obsolete proximally (Pl. II, fig. 2; Text-fig. 6f). The large scales are confined to the posterior 3.5–4.0 mm. of the 20 mm. broad rachis. A few smaller scales occur at 5.0 mm. from the posterior border, and the anterior 15 mm. of the rachis is devoid of scales and fairly smooth. At the anterior margin rudiments of short spines are indicated. More distally, at 70–100 mm., the same large parabolic scales occur near the posterior border. Many of these ventral scales show the characteristic seta socket near the focus of the parabola. The scales, diminishing in size, may be traced anteriorly up to about half the width of the axis.

The dorsal surface of the rachis is shown only in the distal part of the preserved appendage, and here the surface, preserved only as an impression, is smooth except for a few scattered parabolic scales measuring 0.7 mm. in width and 0.4 mm. in length (Text-fig. 6e).

The scales at the posterior margin (Pl. VI, fig. 9; Text-figs. 6d, e, g, h) show rather poorly developed fulcra. More fully developed ones probably occurred on the distal part of the rachis, but this has not been preserved. At the preserved margin the elongate scales, some of them with a well marked seta socket, are enveloping the edge so that one half (usually the larger half) is situated on the ventral side and the other half on the dorsal side (Pl. VI fig. 9). The distal portion of the folded scale gets gradually more prolonged (Pl. V, fig. 8), forming a short fulcrum, one of which has been removed (Pl. V, figs. 9, 10). In ventral view the fulcrum has a narrow triangular outline, a rather flat surface with a longitudinal furrow or sulcus along the distal margin (Text-fig. 6g). On the dorsal side a longitudinal septum or narrow ridge occurs not far from the distal border (Text-fig. 6h). A section which was exposed where the fulcrum was broken off shows that the distal opening or slit between the two folded sides of the original scale, occurs at the distal margin slightly on the ventral side (Text-fig. 6g). The ventral sulcus forms a bed into which the next fulcrum may be partly intercalated.

Appendage E.—This appendage is known through a well-preserved specimen (G.S.E. 9682, Pl. II, figs. 11–15; Pl. V, figs. 6, 7; Pl. VI, figs. 10–13; Text-figs. 7a–g).

Appendage E does not occur in the holotype and it is therefore not possible to decide whether or not it succeeds the last appendage (D) in this specimen. The appendage was probably attached to a basal joint, an indication of which is suggested in a similar appendage of the closely related Belgian species *C. dewalquei* (Pl. III, fig. 19). The rachis of the appendage is flat and differs from the finger-shaped ones by having a longer distally tapering portion, a slightly concave anterior border, and a convex posterior border. The largest width of the rachis is about one-quarter the length. Both surfaces have a distinct ornamentation.

The ventral surface is covered by scales or flat tubercles or areoles, diminishing in size from the posterior to the anterior parts of the rachis (Pl. II, fig. 12). The largest scales have a width of 0.5 mm., the smaller of 0.2–0.3 mm. Their length is more indistinct, but is usually about twice the width. The elongate scales have a semicircular to parabolic, slightly raised distal border. The sides of the scales are parallel or convex giving the scales a more elliptical outline (Pl. V, fig. 7). Seta sockets occur near the focus of the parabola. The scales may develop into flat tubercles or areoles, bordered all round by an elliptical

outline (Pl. II, fig. 12; Text-figs. 7*c, h*). The sculpture differs from that of appendage B which is more eurypterid-like (Pl. I, fig. 17; Pl. II, fig. 7).

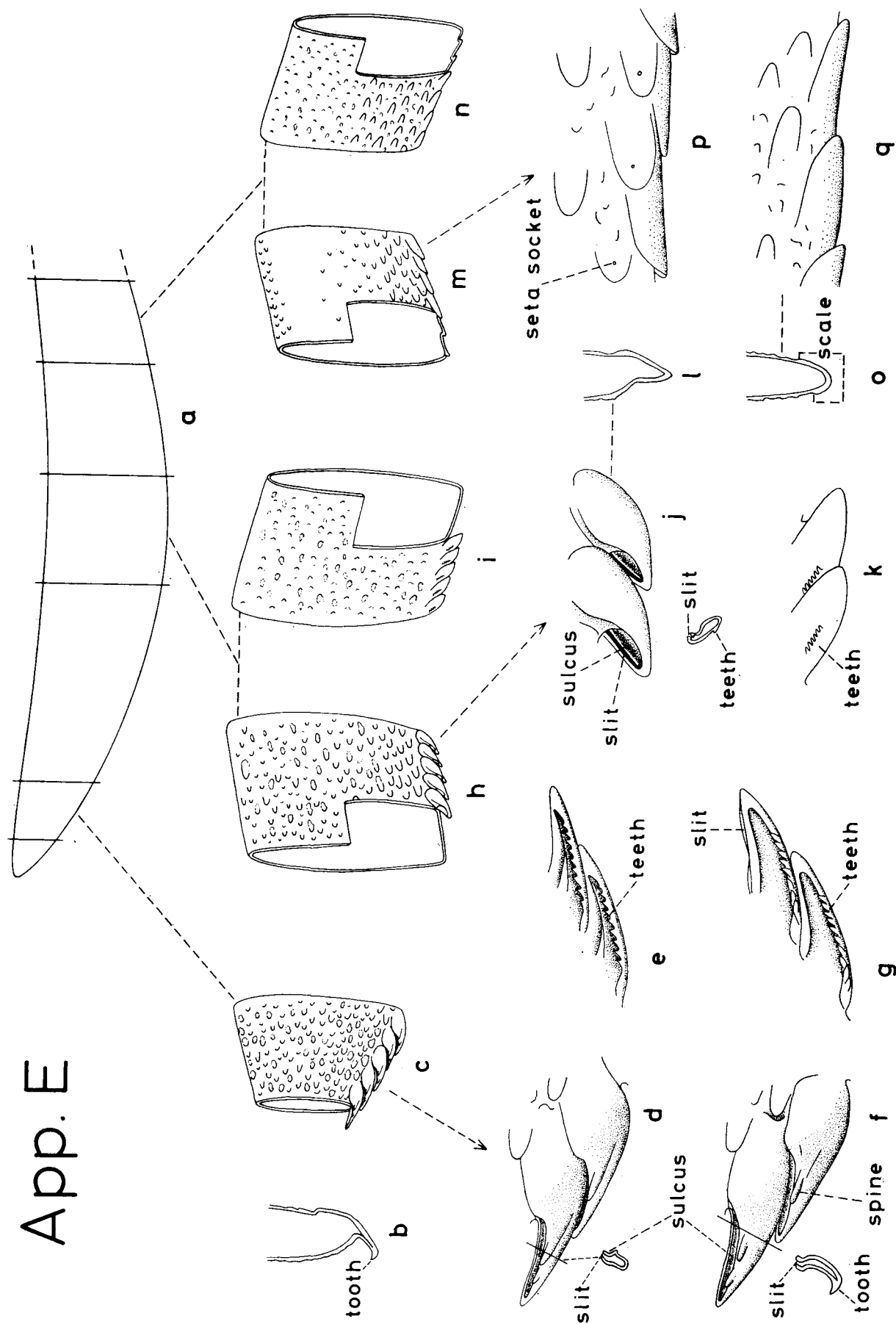
The dorsal surface also has elongate scales; they are somewhat more scattered (Pl. V, fig. 6; Text-fig. 7*m*), the surface in between being irregularly granulated. The scales are elongate of about the same dimensions as on the ventral surface and diminish in size towards the anterior border. Flat elliptical tubercles or areoles are not characteristic, nor seta-sockets on the scales. The dorsal surface has no trace of flat filaments such as are seen in Appendage B.

The development of the fulcra along the posterior margin is well demonstrated in this appendage. In the proximal part of the rachis the posterior margin is enveloped by large scales bent along the median line so that one half is seen on the ventral side and one half on the dorsal side (Pl. V, figs. 6, 7; Text-figs. 7*o, p, q*). Distally the tips of the bent marginal scales tend to be extended in a postero-distal direction forming fulcra. As they are followed distally along the rachis the marginal scales or initial fulcra become more modified and elaborate (Pl. II, figs. 13–15; Text-figs. 7*h–k*). The fulcra get so crowded that they partly overlap each other. In ventral view the distal portion of one fulcrum is covered by the posterior portion of the fulcrum in front (Pl. II, fig. 13). This causes the formation of an S-shaped groove or sulcus along the distal margin, a sulcus which serves as the bed for the proximal portion of the fulcrum distal to it. The original slit between the dorsal and ventral part of the primary scale is more or less closed, leaving only a narrow slit on the ventral side near the distal border (Text-fig. 7*j*). In appendage B the slit is more open and occurs on the dorsal side of the fulcrum (Pl. I, fig. 13; Text-fig. 4*g*). The dorsal part of the fulcrum is flat and smooth, and provided in the basal part with a short fringe with 6–7 teeth directed distally. These teeth may be homologous with the teeth at the proximal margin on the fulcra of appendage B (Pl. II, fig. 10; Text-figs. 4*h, i*). The distal margin of the fulcra in appendage E forms a narrow steep wall (Pl. II, fig. 14).

In a more distal position on the rachis the fulcra become more elongate and dagger-shaped, as in appendage B. The free, narrow portion of the fulcrum is bent in a dorsal direction so that it is only partly visible. In ventral view the long distal prolongation of the fulcrum (Text-fig. 7*d*) may be seen. This portion has a more or less pronounced sulcus (Pl. VI, figs. 11, 12; Text-figs. 7*d, f*) near the antero-distal margin. The slit has returned to the margin and is not visible in ventral view (partly visible in dorsal view as shown in Text-fig. 7*g*). The postero-proximal margin of the sulcus is provided with one or two short spines or knobs (Pl. VI, fig. 12; Text-fig. 7*f*). The basal portion of the fulcrum is smooth and rather flat. The left fulcrum shown in Pl. VI, fig. 10, actually the third from the tip, was removed and is shown in isolation in Pl. VI, figs. 11, 12. The removed fulcrum demonstrates the dorsal surface (Pl. VI, fig. 12; Text-figs. 7*e, g*). The concave dorsal surface is bordered antero-distally by a strong marginal ridge in front of which the slit is partly visible. Along the postero-proximal margin a row of 9 powerful teeth or denticles occurs. The teeth are mainly directed dorsally. These structures are evidently homologous with the intra-marginal teeth on the ventral surface of the more proximal fulcra (Pl. II, figs. 14, 15; Text-fig. 7*k*) and the marginal teeth in the distal fulcra of appendage B (Pl. II, fig. 10; Text-figs. 4*h, i*).

Remarks on paratypes.—1. Specimen G.S.E. 2127, from the Calcareous Sandstone Measures of Lennel Braes, Tweedmill, near Coldstream, Berwickshire, which was not noted by Peach, is of special importance since it shows both appendages A and B *in situ*, each attached to a small basal plate (Pl. II, figs. 17, 18; Pl. III, fig. 1). The appendages belong

App. E



TEXT-FIG. 7.—Appendage E of *Cyrtoctenus peachi* n.g. n. sp. Diagrams showing structure of rachis and fulcrum. a. outline of rachis to indicate position of diagrams c, h, i, m, n; b. section indicating the postero-dorsal direction of fulcrum; c. distal position of fulcrum; d. ventral view of distal fulcrum; e. ventral view of rachis; f. post-ventral view of the same fulcrum; g. anterio-dorsal view; h, i. ventral and dorsal view; j, k. ventral and dorsal view; l. section of fulcrum; m, n. ventral and dorsal view; o. section of rachis; p, q. scales and fulcrum developing at the posterior margin.

to a small individual, the appendage A measuring only 65 mm. in length compared to a restored length of 240 mm. in the same appendage in the holotype. The sub-rectangular basal plate of A has a median length of 7 mm. and a width of 3.5 mm.–4.5 mm. Near the post-proximal lobe of the rachis, the ventral skin of the basal plate has been removed exposing a plate dorsal to it which has a distinct distal margin with a row of small powerful knobs. A section across the basal structures suggests the presence of several cuticulae above each other indicating two different plates below the body wall. A posterior plate shows a distinct ornamentation of very small (0.02–0.06 mm. in width) elongate scale-tubercles directed distally and resembling in shape and size those shown in Pl. III, fig. 18. Near the convex joint-line with the rachis, small and broad (0.05–1.0 mm.) scale-tubercles are present on the plate surface.

The two rows of filaments of A are well seen, there being about 170 in the 65 mm. length of the rachis. The filaments point distally and make an angle with the rachis varying from 30° near the distal point, to 40°–50° in the middle, to 60°–70° in the proximal part of the shaft. In the proximal part a difference in direction of the upper and lower rows of the apparently flexible filaments is noticeable. The length of the filaments is fairly constant, varying from 6 mm. in the middle of the appendage to 4.0 mm. or less near the base and near the tip. Filaments bleached and embedded in Canada Balsam show no distinct peg organs such as in *Gigantoscorpio*.

Appendage B is preserved mainly as a mould, small parts only of the cuticula being present. The basal plate is shorter than that of A to which it abuts. The finger-shaped rachis has a length of 50 mm. and a greatest width of 6.0 mm. The rachis shows a short postero-proximal process and the posterior margin is provided with fulcra along the distal third. As shown in Pl. II, fig. 17, the ventral cuticula with the fulcra has been displaced and covers the anterior border of the rachis. The ventral surface of the rachis has parabolic scales or scale-tubercles, broader than those of A. On the dorsal surface minute tubercles are suggested but not well preserved. The fulcra resemble those of B in the holotype.

Judging from the disposition of the basal plates the two rachi probably were directed outwards and backwards as suggested in Text-fig. 10.

2. Specimen G.S.E. 2183, from the Calciferous Sandstone Measures of the River Tweed at Coldstream Bridge, Berwickshire, shows details of appendage A (Pl. III, figs. 2–3; Pl. VI, fig. 7) and the impression of a body plate (Pl. III, fig. 6), probably a tergite.

The basal portion of the appendage is missing; the length of the rachis preserved, however, is 96 mm. and its width at the base is 8.2 mm. It tapers gradually towards the distal tip where it ends in a point. The rate of curvature increases distally so that the tip of the rachis is parallel to the distal filaments and in the last 9 mm. is the same width as the filaments. The surface of the rachis is well preserved showing the characteristic scattered elongate scale-tubercles, each having a blunt semicircular raised distal margin (Pl. III, figs. 2, 3). The sides of the scale-tubercles are parallel or slightly convex, steep and at the distal margin may overlap the surface below by 0.1 mm. The height of the distal margin varies from very little up to 0.15 mm. The width of the scale-tubercles varies from 0.1 mm. to 0.2 mm. and the length from 0.6 mm. to 1.2 mm.

This specimen exhibits well the elaboration of the scale-tubercles in the distal portion of the rachis. Denticles are present along the narrow, most distal portion of the rachis, somewhat similar to those occurring on the filaments. At 10 mm. from the tip it is evident that these denticles are formed by elongate scale-tubercles and at 20–40 mm. from the tip these denticles are replaced by flat spines 1.5 mm. to 3.0 mm. in length, directed distally

and forming an angle of about 20° with the direction of the anterior margin of the rachis (Pl. VI, fig. 7). The spines are generally flat with a slight concavity towards the anterior margin and may overlap one another by as much as one half of their length. A spine removed from the rachis displayed a longitudinal carina on both upper and lower sides, apparently formed by a combination of smaller tubercles of the type found on the surface of the rachis.

The two rows of filaments are well exposed, the filaments having a length of 33–34 mm. and forming, in the proximal part, an angle of 55° with the rachis which decreases distally until at the tip the filaments are parallel with the shaft (Pl. III, fig. 2). The filaments are set *en echelon* with the rachis (Pl. III, fig. 8) forming an angle of about 60° with the surface of the rachis at their base. The basal two-thirds of the filaments have a fairly constant width of 1.1 mm. but they taper gradually towards a sharp point (Pl. III, fig. 4). On the outer surface their basal portion may have one or two longitudinal ridges parallel to the margin facing distally, while on the inner surface they have inwardly directed marginal denticles. The denticles become submarginal near the base and do not continue in the narrow part of the filament towards the tip. Outwardly directed marginal denticles as shown by G.S.E. 2144 (Pl. III, figs. 9, 10) are virtually absent in this specimen.

Associated with the appendage is a large fragment of body plate (Pl. III, fig. 6) described below.

3. Specimen G.S.E. 2144 (Pl. III, figs. 9, 10, 12) from the Calciferous Sandstone Measures of Lennel Braes, Tweedmill, Coldstream, Berwickshire, exhibits details of the filaments of appendage A (Pl. III, figs. 5, 9, 10, 12). Their width, up to 1.2 mm. indicates that the specimen belongs to a large individual of the same size as the holotype. The flat or concavo-convex flexible filaments vary in thickness from 0.03 mm. to 0.08 mm. and a thickening of the margins is often present. The distal facing margin may be bent inwards more or less, and in this case a longitudinal ridge is often formed on the outside surface (Pl. III, figs. 9, 10). The ridge may not be continuous but divided up into elongate scale-tubercles (Pl. III, fig. 10), not unlike those on the rachis. In one case scattered elongate drop-like scale-tubercles have been observed outside the line, which may themselves develop into a continuous ridge. On the inner side a row of denticles is developed which starts about 2.5 mm. from the base of the filaments. At the base the denticles are insignificant and the row is intra-marginal being 0.25 mm. from the margin; further up the filament the inwardly directed denticles become more powerful (Pl. III, fig. 12), and at a distance of about 15 mm. from the base, the denticles become marginal with a distal direction nearly corresponding to the outer surface of the filament (Pl. III, figs. 9, 10). The denticles are about 0.3 mm. apart but some 15 mm. from the tip of the filament they become more openly spaced at about 1.0 mm. or more apart, and towards the extremity the filament is devoid of denticles. Where the denticles are well spaced at the narrow part of the filament, similar denticles may develop along the other margin.

4. Specimen G.S.E. 5864 (Pl. III, figs. 7, 13–16, 18) from the Calciferous Sandstone Measures of the River Tweed, Coldstream Bridge, Berwickshire, also shows details of the filaments of appendage A, and their oblique insertion into the posterior margin of the rachis. Filaments in a distal position on the rachis have a width of 1.15 mm., while more proximally, where their width is only 0.8–0.9 mm., they taper more rapidly from the base (Pl. III, figs. 13–15). The detached specimens show the basal aperture into the hollow but compressed filaments (Pl. III, figs. 14, 15). The internal row of denticles starts near the mid-line of the filament as a faint ridge which becomes differentiated into denticles as the row gradually

approaches the margins where the denticles change direction. In the distal filaments the denticles become marginal very soon. The longitudinal intra-marginal ridge on the outer surface of the filaments is generally well developed, but may also appear as a row of elongate scale-tubercles with a length of 0.6 mm. and widths of only 0.05–0.07 mm. The “head” of the scale-tubercles is blunt, not flattened with a sharp distal margin, such as on the rachis.

When the calcareous shale was dissolved to release the filaments a piece of thin yellow cuticula was found which might represent a part of an intersegmental membrane (Pl. III, fig. 18). The surface shows a distinct ornamentation of close-set knob-like scale-tubercles with a width of 0.02 mm. to 0.03 mm.

5. Specimen G.S.E. 12298 (Pl. VI, figs. 3, 4, 6) from Longcraigs Bay, East of Belhaven Bay, Dunbar, exhibits an incomplete detached appendage B seen in ventral view. The preserved portion of the rachis is 105 mm. in length being slightly deficient at both proximal and distal ends. Over most of its length the finger-shaped rachis is almost straight, tapering from a width of 18 mm. at the proximal end to 14 mm. at the point where it is broken off distally. At the proximal end the form of the posterior border is seen to continue beyond the portion of the rachis which is preserved and swings posteriorly to form a rather strong concave curve. The ornament of the ventral surface of the rachis is closely similar to that of the holotype, parabolic scales being developed, particularly in its distal and posterior portions. Many of the scales carry a circular seta socket (Pl. VI, fig. 6; c.f. Text-fig. 5). Fulcra, developed at the distal portion of the posterior border of the ventral surface, are well seen. All or part of 16 fulcra are displayed in the distal 28 mm. of the border. These show the progression from the ridged condition (Text-fig. 4g) to the sulcate condition (Text-fig. 4h) in which 11 or 12 teeth are developed on the proximal margin of the fulcra (Pl. VI, fig. 4).

In parts the substance of the rachis has been broken away to reveal an external cast of the dorsal surface below. This shows that the ornamentation of the dorsal surface of the rachis agrees closely with that of the holotype. Midway along the rachis there are narrow raised triangular scale-tubercles which become larger and more paraboloid distally, a condition well seen near the distal break where the scales are more crowded in the posterior half of the rachis. The ventral surface has been broken away in the mid-section of the posterior border to show the protrusion of the filaments from their points of origin some distance from the posterior border of the dorsal surface. There are seven to eight filaments in each 10 mm. of the margin in the area exposed, their greatest observed length being 9 mm. The disposition of the filaments is as described for the holotype. The proximal 30 mm. of the posterior border of the rachis is smooth, filaments being absent.

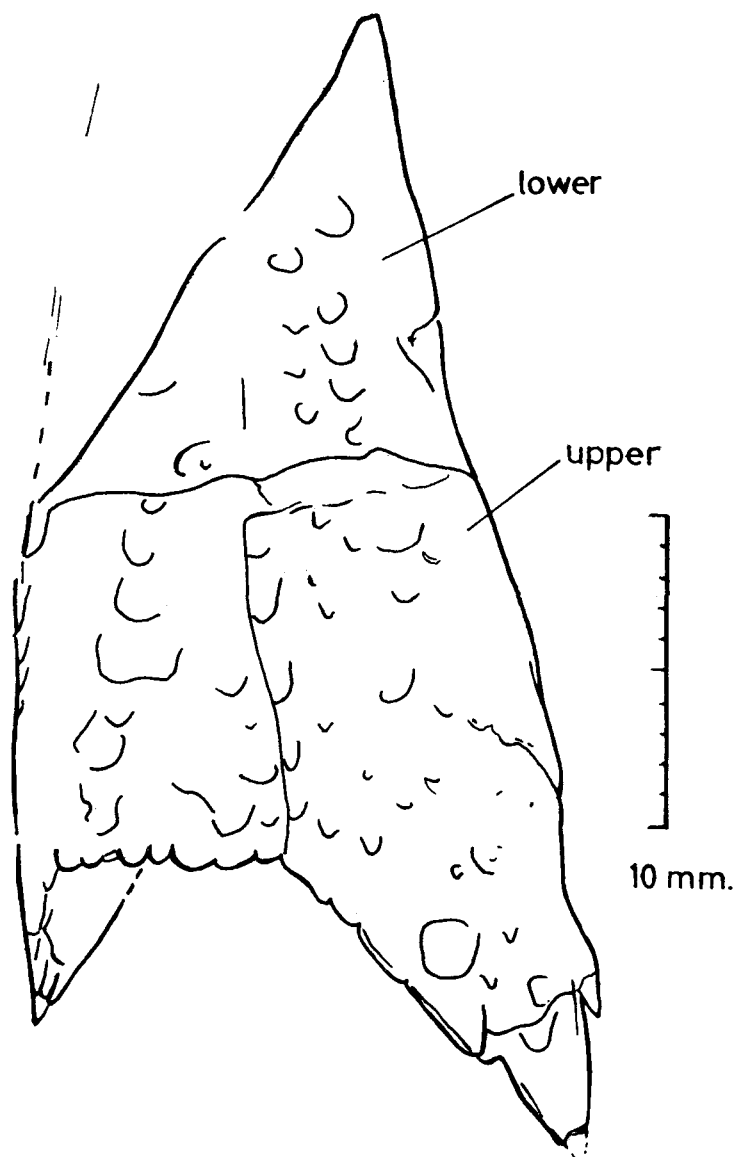
6. Specimen G.S.E. R.1729 (Pl. VI, fig. 3, Text-fig. 5) from the Calciferous Sandstone Measures of Coomsdon Burn, Northumberland, shows a particular twisting of the proximal portion of the filaments.

Other fragments probably belonging to the species

In addition to the appendages described above, the Scottish material contains a few specimens which belong to other parts of the arthropod.

Tergite.—Specimen G.S.E. 2183 shows a well preserved appendage A (Pl. III, figs. 2–4) resting on a large fragment of a body plate (Pl. III, fig. 6) having parts of the straight anterior and posterior margins preserved giving a segmental length of 47 mm. The greatest preserved width is 92 mm. The left margin is straight and its position suggests that the sides of the

plate converge slightly anteriorly. The ornamentation is preserved as an impression, but a small piece of the cuticula was preserved and has been mounted in Canada Balsam. Near the anterior border the ornamentation consists of parallel ridges 0.6 mm. to 3.0 mm. in length, the distance between the ridges being 0.2 mm. to 0.4 mm. Posteriorly the transverse



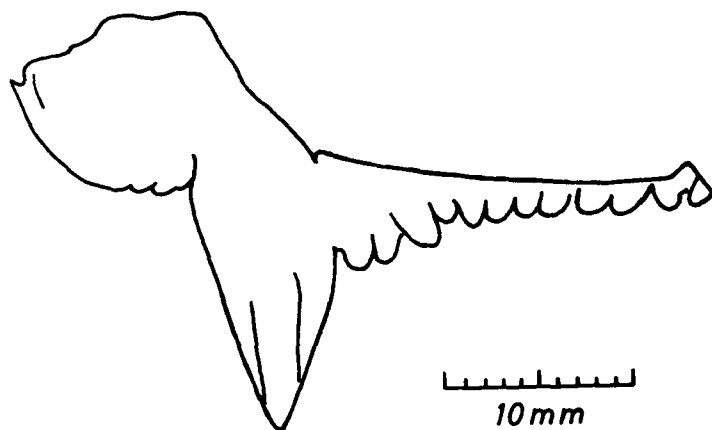
TEXT-FIG. 8.—Possible segment of prosomal appendage in *Cyrtoctenus peachi* n.g. n.sp. G.S.E. 2180.

ridges change into transverse crescent scales with a width of 1.2 mm. to 1.5 mm. and a length of only 0.2 mm. The removed cuticula appears to be smooth on the inner surface indicating that the ridges are not associated with corresponding grooves on the inner side. The posterior part of the plate has no scales. The ornamentation is very similar to that of the genus *Pterygotus* among the eurypterids.

Segments of prosomal appendages (?).—G.S.E. 2180 demonstrates a segment of a large, probably prosomal, appendage which may belong to *Cyrtoctenus peachi* (Pl. III, fig. 17; Text-fig. 8). The subtriangular piece is broken off obliquely in the proximal end. The distal end has a marked indentation. The slightly convex sides diverge distally. The distal

corners are formed by two large flat spines, flanked by smaller spines, and the indented part between them has indications of marginal scales or blunt spines. Two surfaces of the flattened specimen are preserved. Both sides are provided with knobs, mainly arranged in two rows parallel to the diverging sides of the segment.

On the holotype, G.S.E. 2185, a fragment of a denticulate plate has been excavated (Pl. V, fig. 11; Text-figs. 7, 9). The fragment represents a plate of unknown shape having a characteristic margin with powerful teeth. To the left of the large central tooth as shown in Pl. V, fig. 11 there are 12 smaller teeth of about the same size forming a straight but rather uneven margin. Of these the three teeth to the right, that is those next to the large central tooth, protrude in relation to the others. Each tooth measures 1.3 mm.–1.9 mm. in width.



TEXT-FIG. 9.—Serrate margin of plate, possible segment of prosomal appendage in *Cyrtoctenus peachi* n.g. n.sp. G.S.E. 2185.

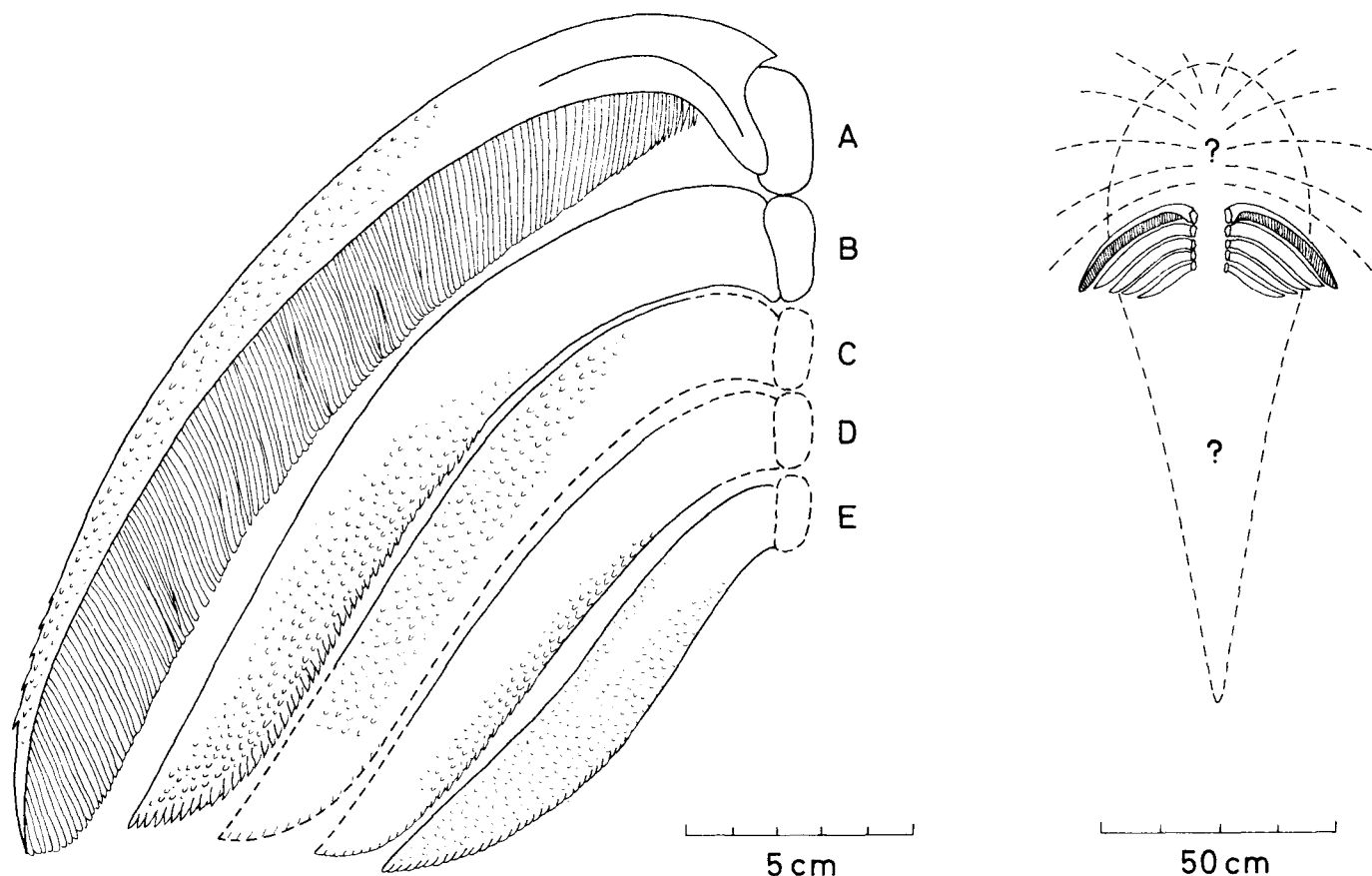
The free more or less semicircular portion is short but the lateral margins of the tooth continue on the surface of the plate giving a subrectangular outline to the structure. The length of the tooth, including the portion of the plate, is about twice the width. In the present state of preservation the smooth teeth are flat. In cross-section a thick upper cuticula and a thick lower cuticula are separated by a distinct line marking a plane along which the upper cuticula is easily split off from the lower.

At the middle of the margin a larger triangular tooth or flat spine is developed. The lateral slightly convex sides converge and meet at the distal, not sharp point. On the lower surface a longitudinal line near the left margin indicates a sharp edge on the otherwise smooth surface. To the right another line suggests a furrow. The upper surface of the flattened spine is slightly concave, the lateral borders being elevated. The lower surface has a corresponding slightly convex surface. This might be due to preservation.

The right portion of the margin is convex. At the margin this portion of the plate does not directly abut on to the large spine but is preserved at a slightly higher level. However, further back the two surfaces pass into each other showing that the large spine and the convex margin belong to the same plate. To the left, near the large spine, the margin has a few short teeth measuring about 1.3 mm. across, and with a free portion only about 0.6 mm. long. Only the three first teeth are distinct; further on they gradually disappear and are replaced by a smooth margin. The cuticula along this margin is exceptionally thick measuring apparently up to 0.15 mm. The left tooth is short, parabolic and slightly pointed. The convex surface differs decidedly from that of the other teeth. The surface has

numerous close set scales with raised distal margins. The width of the scales is about 0.2 mm., their main direction being more or less perpendicular to the margin formed by the 12 teeth. Similar scales of the same size and arranged as in eurypterids, occur on a small area beyond the base of the large tooth; otherwise the surface has no scales.

The fragment described probably represents only a portion of the original plate. The denticulate margin might have been longer in the complete plate. The size of the arthropod



TEXT-FIG. 10.—Tentative reconstruction of the abdominal appendages in *Cyrtoctenus*. Ventral view. The position of the appendages on the unknown body is suggested to the right.

plate and its occurrence in close connection with the other arthropod remains seem to exclude the possibility of the plate belonging to some other form. With regard to the nature of the plate several possibilities may be discussed: 1. The powerful teeth might recall those along the inner margin of the large chelicera of pterygotid eurypterids (Størmer 1955, p. 32, figs. 1c, 2b, 3b; Waterston 1964, p. 28, fig. 5). However, the shape of the portion of the plate to the right of the large tooth deviates decidedly from the end of the chelicera. 2. In the largest eurypterids such as the Pterygotidae the last coxa (VI) in particular has powerful teeth along the margin facing the mouth. In *Pterygotus* (Clarke and Ruedemann 1912, Pl. 79, fig. 1) the first tooth is larger than the others which, however, have about the same shape. Our specimen differs in having more symmetrical teeth and a larger non-denticulate margin on the right side of the large tooth. 3. The posterior margin of the tergites of some eurypterids may be prolonged into post-lateral spurs. Since the large tooth is not lateral it cannot be interpreted as a normal post-lateral spur of a tergite. Interlateral spurs have recently been noted, however, by Waterston (1968) in *Dunsopterus* and *Vernonopterus*. It might thus be possible that the fragment represents part of the posterior margin of a tergite.

4. A more probable solution seems to be that the fragment represents the margin of one of the segments of a prosomal appendage. The segment described above (Pl. III, fig. 17; Text-fig. 8) has a similar serrate margin with a large tooth. If a similar segment or joint had been compressed differently an appearance like that of the present fragment could result.

Reconstruction

Text-fig. 10 suggests a reconstruction and arrangement of the better known parts of *Cyrtoctenus* based on the structures described in the type species *C. peachi* nov. We know very little of the anatomy except for the five pairs of appendages of which the fifth one probably succeeds the fourth. The structure of the appendages indicates that they belong to the anterior portion (mesosoma) of the abdomen. The comb-like appendage A is probably post-opercular and may belong to the same somite (9th) as the pectines of the scorpion. Fragments, probably belonging to the jointed prosomal appendages, occur.

Particularly on account of its large size it is reasonable to suppose that *Cyrtoctenus* must have been an aquatic animal. The gills may have been situated on the ventral body wall above the appendages as in eurypterids (Wills 1965), although in eurypterids the ventral abdominal appendages are plate-shaped.

We know nothing about the shape of the body, besides fragments of plates suggesting tergites of a more or less eurypterid type. In the reconstruction an oblong body is suggested in the style of a generalised eurypterid. The size is based on the large holotype.

(b) *Cyrtoctenus dewalquei* (Fraipont)

Pl. III, figs. 19–21; Pl. IV, figs. 1–2, 3?, 4?, 5–12; Pl. V, figs. 12?, 13?, 14–19; Pl. VI, figs. 14, 15; Text-fig. 11.

Eurypterus (?) *Dewalquei*, Fraipont *partim* Fraipont 1889, pp. 58–62, Pl. II, figs. 8, 9; possibly also figs. 4–7.

Eurypterus (?) *Dewalquei* var. *longimanus* Fraipont 1889, p. 61, Pl. II, fig. 10.

Eurypterus (?) *dewalquei* O'Connell, 1916, p. 39.

Eurypterus (?) *dewalquei* var. *longimanus* O'Connell, *ibid.*, p. 39.

Eurypterus Dewalquei Diener 1924, p. 16.

Eurypterus dewalquei Størmer 1936, p. 33.

Eurypterus dewalquei var. *longimanus* Størmer, *ibid.*, p. 33.

Lepidoderma (?) *dewalquei* Kjellesvig-Waering 1948, p. 10.

Adelophthalmus (?) *dewalquei* Kjellesvig-Waering 1958, p. 1140.

Non

Eurypterus (?) *Dewalquei* Fraipont 1889, Pl. II, figs. 2, 3.

Lectotype: R.E. 14783A with counterpart R.E. 14783B, from "Psammites du Condroz" Famennian, Pont-de-Bonne-Modave, Belgium.

From the original collection Fraipont (1889) described arthropod remains which he interpreted as eurypterids. He described the following forms:

(1) "*Eurypterus Loheste Dewalque*" which may be a stylonurid eurypterid (considered as perhaps referable to *Adelophthalmus* by Kjellesvig-Waering 1958); (2) a new species which he named *Eurypterus* (?) *Dewalquei*; and (3) a new variety which he named *Eurypterus* (?) *Dewalquei* var. *longimanus*. This material, together with a considerable quantity of additional material collected by P. Destinez in 1890, belongs to the Laboratoire de Paléontologie Animal of the University of Liège. Through the courtesy of Professor G. Ubahgs

this large collection was sent to Oslo for further study. Most of the specimens in the collection are fragmentary and difficult to determine but some have been valuable in enabling a fuller description of this species to be made.

Fraipont's description of *Eurypterus* (?) *Dewalquei* is based mainly on one specimen, apparently not well preserved, represented in his Plate 2, figure 3 *loc. cit.* This appears to be the anterior portion of the abdomen rather than the prosoma or cephalo-thorax as assumed by Fraipont. The surface of the integument is said to be provided all over with "petit tubercules épineux, subtriangulaires, à pointe dirigée en arrière" (Pl. 2, fig. 3 *loc. cit.*). This specimen, although clearly regarded as important by Fraipont, was not designated the holotype by him and Professor Ubaghs informs us that it is now evidently lost. As pointed out by Kjellesvig-Waering (1948, p. 10) it is most probable that this specimen should be assigned to *Adelophthalmus* (= *Lepidoderma* auct.).

Of the syntypes figured by Fraipont only those represented in his Plate 2, figs. 9 and 10 have been identified in the existing material and of these the most informative specimen is that figured as the holotype of his variety *longimanus* in fig. 10 (R.E.14783). Since *E.* (?) *dewalquei* var *longimanus* is conspecific with *E.* (?) *dewalquei sensu stricto*, the varietal characteristic being simply the greater extent of the appendage which has been preserved. We here designate R.E. 14783 as lectotype of *E.* (?) *dewalquei* which, as revised by us, must be placed in the genus *Cyrtoctenus* nov. The most characteristic specimen of the species is the appendage A, preserved in part and counterpart R.E. 14786 (Pl. IV, figs. 1, 2) which belongs to the later collection.

Diagnosis.—Cyrtoctenid in which appendage A has about 110 filaments in each row of the comb.

Description:

Appendage A.—Specimen R. E. 14786 A and counterpart B (Pl. IV, figs. 1, 2) shows a comb lacking only the basal portion. The scythe-shaped rachis has a convex anterior margin, somewhat more evenly curved than in *C. peachi*. The length of the shaft preserved is 75 mm. and when complete might have measured 85 mm. It tapers gradually towards the distal point. Near the base the shaft has a thickness of up to 0.35 mm. as now preserved. The posterior margin of the shaft is provided with two rows of filaments, about 110 filaments comprising each row, and both rows are visible in parts of the specimen (Pl. V, fig. 14). The angle of attachment of the filaments in the plane of the rachis varies from 40° up to 90° at the proximal end of the shaft, the average being about 45°. Each filament is inserted into the shaft, normal to the plane of the rachis, at an acute angle opening distally as in *C. peachi*. The proximal filaments are quite short, those in the middle have a length of about 11 mm., the distal ones reaching about 6 mm. long. Their width is about 0.3 mm., but less at the tapering distal ends. The filaments are flat with, at the margin facing the tip of the shaft, a narrow rim having a width of about 0.07 mm. This rim is bent inwards forming an angle of about 150° with the main surface of the shaft being more distinct and more bent than is usual in *C. peachi* (Pl. III, fig. 9). Chiefly because the black skin of the filaments is practically absent, only very faint traces of marginal teeth are preserved. In specimen R.E. 14757, representing a fragment of the comb, there are definite traces of the teeth, the distance between succeeding teeth being 0.25 mm.

The sculpture of the shaft consists of elongate and short scales of variable size. Near the anterior margin the scales are elongate with a length up to 0.5 mm. and a corresponding

width of 0.3 mm. Only 1 mm. from the margin the width of the elongate scales diminishes to less than 0.1 mm., and scales of this size are found across the shaft to the posterior margin with the filaments. The scales described are similar to those of the Scottish specimens.

Appendage D (?).—Specimen R.E. 14731 A, B comprises the distal portion of a blunt, probably finger-shaped, appendage (Pl. III, figs. 20, 21). The anterior margin is slightly convex, the lateral and distal parts of the posterior margin are well rounded, the more proximal part being fairly straight. The width of the rachis is 18 mm. The presumed dorsal surface is provided with scattered elongate scales with a width of 0.4–0.5 mm. The scales are confined to the posterior 3.0–3.5 mm. of the rachis. The presumed ventral surface is less well preserved, but short elliptical scales or flat tubercles occur close to the posterior margin.

Well developed fulcra occur only in the more distal portion of the rachis. They are not well preserved, but appear to be dagger-shaped.

Because of the ornamentation and slight development of the fulcra, the appendage described might be appendage D.

Associated with the described specimen of appendage A are two elongate fragments showing a distinct ornamentation. One has distinct parabolic scales similar to those found in appendage D of *C. peachi* (Pl. II, fig. 2). The other fragment (Pl. VI, fig. 14) is finger-shaped and at the margin occur numerous distinct, nearly elliptical scales with well marked seta sockets. This fragment differs apparently from appendage D, and may possibly belong to appendage C of which we do not know the posterior part of the rachis in *C. peachi*.

Appendage E (?).—The lectotype R.E. 14783 A, B (Pl. III, fig. 19; Pl. V, figs. 15–19) comprises a finger-shaped appendage, complete except for the most basal portion. An extra elongate plate in front has a position which might suggest the rachis of an anterior appendage. However, its surface has scales which are directed in the opposite direction to the complete appendage, showing that the shaft in this case had been turned 180°. Another small plate at the base of the rachis might possibly represent a base joint of the appendage, but the preservation is not good enough to decide this. The main shaft or rachis with a maximum width of 14.5 mm. has an outline very similar to that of the appendage E (?) in *C. peachi* and the sculpture is also the same. The elongate scales in the basal portion of the appendage are well demonstrated on the presumed ventral side (Pl. V, figs. 18, 19). The scales have a slight posterior direction near the border where they develop into fulcra which become more prolonged towards the tip of the rachis (Pl. V, figs. 19, 18, 17). The fulcra have the characteristic shape demonstrated in *C. peachi* (Text-fig. 7). The dorsal surface of the fulcra is less well preserved. A flat surface is indicated (Pl. V, figs. 15, 16).

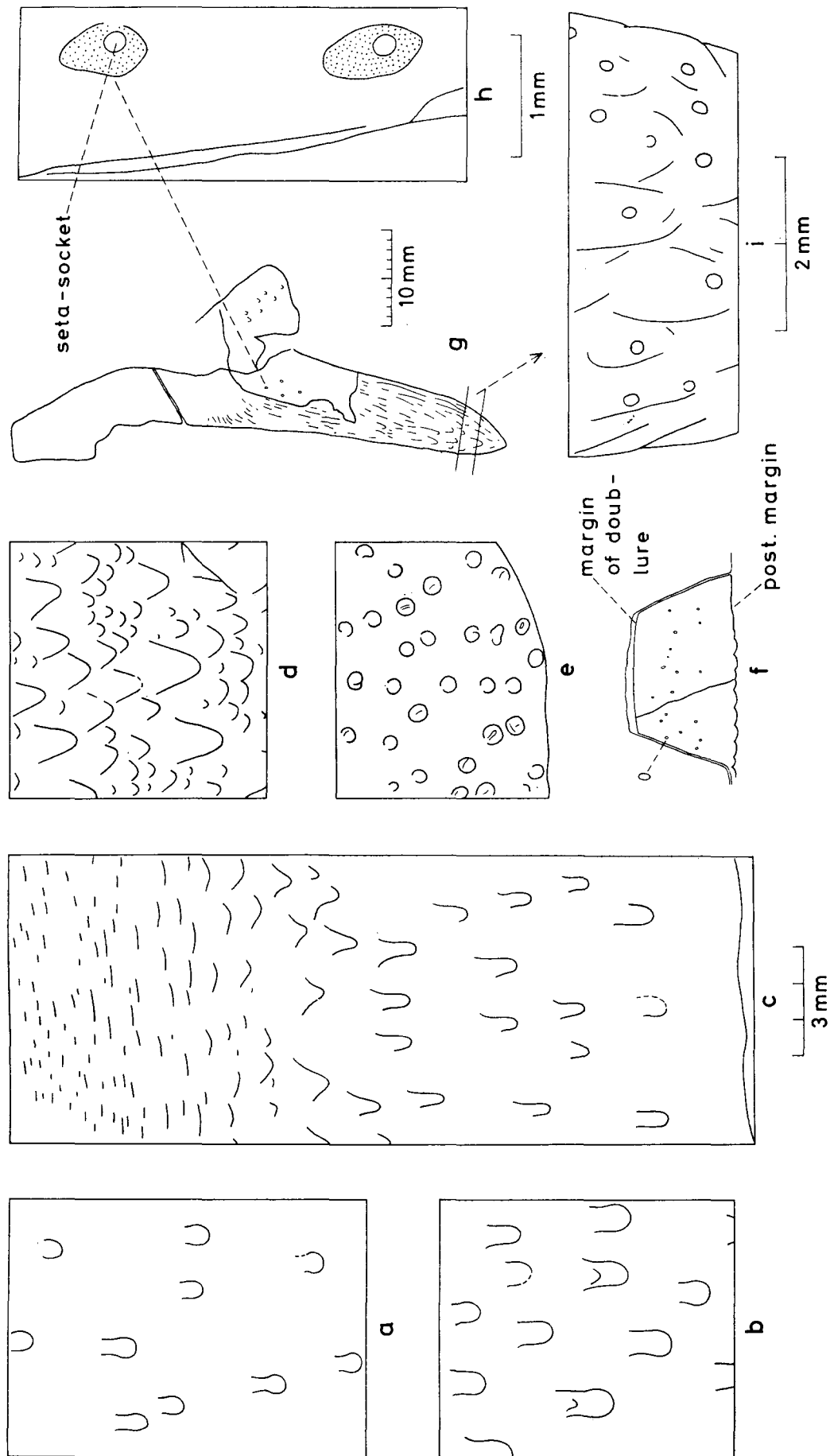
*Other fragments possibly belonging to *Cyrtoctenus dewalquei**

The many fragmentary plates preserved in the Belgian collections usually consist of thin films and show little of the original outline of the plates. The reason for this might be that the original exocuticula contained calcium carbonate which was dissolved before or after the skin was completely embedded in the sediment. Such a selective diagenesis has been assumed by Richter (1931) and Størmer (1934a) in the preservation of certain arthropods. In association with the thin films preserved, calcite plates may occur with a thickness of 0.1–0.8 mm. which are probably secondary fillings between the shell surfaces. The calcite crystals seem to be orientated normal to the surface of the integument. Carbonaceous material occurs which probably represents the carbonised exocuticula.

Abdominal plates.—A large plate, R.E. 14770A (Pl. IV, fig. 8) probably represents a

tergite. The length of the plate is about 65 mm.–70 mm. and the largest width preserved amounts to 170 mm. The complete tergite might have had a width of about 225 mm. The middle part (right in fig.) and a triangular anterio-lateral area are smooth, while the rest of the plate is covered with large knobs or indistinct scales measuring 2.0–2.5 mm. in width and 3 mm. in length. In the left part of the plate the indistinct scales have a postero-lateral direction. Another large plate, R.E. 14777A (Pl. IV, fig. 9) may also represent a tergite of the abdomen. The transverse margins are rather well marked; a slightly convex lateral margin is also indicated (to the left in fig.). The median length of the plate is 66 mm., maximum length 70 mm., and the largest width preserved is 175 mm. Most of the surface of the plate shows no sculpture. However, in the upper left corner of Pl. IV, fig. 9 the impression of the sculpture is well preserved on a narrow strip of the skin. The sculpture consists of scattered scale-tubercles of a characteristic inverted keyhole shape (Text-fig. 11a). The length of the scale-tubercles is 1.5 mm., or less if the basal portion is not seen. The width of the “head” (the distal portion) is 0.6 mm., the “neck” is 0.3–0.5 mm. and the basal portion somewhat wider. As shown below, the “head” or distal portion of the modified scale points posteriorly. The orientation of the scale-tubercles shows that the plate, the probable tergite, has been figured upside down. Remains of other tergites occur close to the one figured. R.E. 14744, a plate fragment measuring 65 mm. × 40 mm., (Pl. IV, fig. 5; Text-fig. 11b) shows a similar sculpture. The drop-like scale-tubercles have a less constricted neck, but the size, and the space between the scale-tubercles, are about the same.

The derivation of the oblong scale-tubercles is well demonstrated in two smaller tergites (?). The length of one of the tergites (Pl. IV, fig. 12) is 24 mm., and of the other 32 mm. The greatest preserved width is 57 mm. Along the posterior margin of the smaller specimen the skin has been removed showing a narrow doublure forming a 2.9 mm. wide brim (Text-fig. 11f). The doublure is smooth with a few small tubercles appearing as relatively deep holes in the impression preserved. The small slightly oblong tubercles have a length of 0.1–0.15 mm. Small crescent-shaped plicae are present along the posterior margin. An impression of the larger tergite shows very well the sculpture of the skin (Text-fig. 11c). Near the anterior border, small, and very slightly curved, eurypterid scales are indicated having a width of about 0.3 mm. Passing posteriorly the scales gradually become larger (0.7–1 mm.) and more crescent-shaped. About 12 mm. from the posterior margin the scales become triangular and change into mucrones. Further on the sides of the triangular mucrones become concave, and the distal portion is prolonged into a narrow oblong scale-tubercle. Thence the sides of the scale-tubercles are almost parallel and the basal portion but slightly broader than the distal raised portion. The distal margin is steep. A distal row of scale-tubercles occurs 2 mm. from the margin. These scale-tubercles are broader than the others, having a width of 0.7 mm. as against 0.3 mm.–0.4 mm. of those in front of them. Some of the posterior scale-tubercles have a distinct inverted keyhole shape, similar to that of the ones described above. These structures demonstrate clearly the transition from *Hughmilleria-Pterygotus* scales to the characteristic scale-tubercles shown in several different plates. The same ornamentation is seen in R.E. 14742 (Pl. IV, fig. 7) in which some of the narrow scale-tubercles have a length of over 3 mm. More of a transition into mucrones is shown in R.E. 14735 (Pl. IV, fig. 11) and typical elongate eurypterid scales occur in R.E. 14739 (Pl. IV, fig. 10; Text-fig. 11d). These well-preserved scales occur on the surface of a 0.2–0.8 mm. thick plate. In cross-section it seems to consist of two sets of calcite crystals meeting midway between the two surfaces. The ornamentation consists of larger and smaller scales, the latter occurring in between the larger ones, often in larger



TEXT-FIG. 11.—Ornamentation of plates possibly belonging to *Cyrtactenus dewalquei* (Fraipont). a, b, inverted "keyhole" scale-tubercles; c, transition from short transverse ridges—crescentic scales—triangular scales—inverted "keyhole" scale-tubercles; d, "Pterygotus" scales; e, knobs or composite tubercles; f, double of tergite (?) with small pits; g—i, process of plate carrying numerous seta sockets, those in the basal part surrounded by pitted area (h); i, magnified part bordered by crossing lines in g.

numbers as shown in the upper right corner of Pl. IV, fig. 10. The larger scales are subtriangular to parabolic in outline; the sides may be slightly concave. The raised distal portion of the scales ends in a steep wall. The width at the base runs up to 1.5–1.6 mm., the largest length up to 1.5 mm. The smaller scales are shorter and more crescent-shaped, the basal width being about 0.5–0.6 mm., and the length 0.3–0.5 mm.

Another kind of ornamentation is demonstrated in R.E. 14776B (Pl. IV, fig. 6; Text-fig. 11e). The surface of the skin bears numerous scattered tubercles with a circular outline and a diameter of 0.3–0.6 mm. Some of the knobs or tubercles apparently have crossing furrows on the top, suggesting the presence of composite tubercles such as are known in *Gigantoscrapio* (Størmø 1963, p. 83).

Discussion on scales and tubercles

Many of the fragments preserved in the Belgian material show characteristic sculpturing. The most common is the "inverted keyhole structure" (Text-figs. 11a, b). Since these elongate scale-tubercles occur in so many specimens, among them the large plates which probably represent tergites, it is reasonable to assume that they belong to *Cyrtoctenus dewalquei*. Certain specimens (Text-fig. 11c) have clearly demonstrated the transition between the "keyholes" and typical eurypterid scales. Scales of eurypterid (*Pterygotus*-) type are found also on a large plate referred to *C. peachi* described above (p. 79–80). Subtriangular scales of various sizes also occur (Text-fig. 11d) which may belong to *Cyrtoctenus*, but may also belong to some kind of eurypterid. Characteristic of these scales and of those forming a transition between the crescent-shaped ones and the keyhole scale-tubercles is the tendency to form concave lateral margins of the triangular scales. Various kinds of knobs or tubercles also occur (Text-fig. 11e; Pl. IV, fig. 6).

The structures described resemble closely the sculpture found in certain eurypterids, particularly in more or less contemporaneous Carboniferous species. In *Dunsopterus stenosoni* (R. Etheridge jun.), redescribed by Waterston (1957, p. 282, Pl. 3, figs. 1, 2; 1968, Pl. 1, fig. 5), one finds a transition from ordinary crescent-shaped scales into triangular to narrow mucrones with concave lateral margins. Although the narrow mucrones do not show the "keyhole" structure, and do not reach the posterior margin of the supposed tergite in *Dunsopterus*, the correspondence with *Cyrtoctenus* is very striking. Another similarity is the great size. However, although *Dunsopterus* exhibits morphological features which may suggest its inclusion in the Stylonuracea among the eurypterids, our knowledge of the genus is so limited that it may yet prove to belong to a different arthropod group.

The typical mucrones or triangular scales of varying sizes (Text-fig. 11d) may be matched in well-known Carboniferous eurypterids such as *Adelophthalmus mansfieldi* (C. E. Hall) (Hall 1884, Pl. V, fig. 7 for narrow triangular scales and Pl. V, fig. 8 for rounded scales of varying size.)

We may conclude that the sculpture of plates probably belonging to *Cyrtoctenus* show affinities to structures found in eurypterids, and particularly to certain large Carboniferous species whose anatomy is too incompletely known to be quite sure of their eurypterid affinities.

Incertae sedis

Two specimens, which occur in the Belgian collections with *Cyrtoctenus dewalquei*,

are of uncertain position and are here described because of their possible association with that species.

The first is a spine (R.E. 14728A and B, Pl. IV, fig. 3; Pl. V, figs. 12, 13; Text-figs. 11g-i) attached to a basal plate-like portion. The plate-like base is fragmentary but shows a straight lateral margin and a tuberculate surface, which occurs beside the base of the spine but not directly attached to it, and is formed apparently by an extension of the basal plate. The plate has an exposed length of 30 mm. which may possibly have been the length of the segment to which the spine was attached. The length of the well-preserved finger-shaped spine is 24 mm. The spine shows characteristic ornamentation. In the proximal part it consists mainly of striae, but a part of the surface in the proximal portion, which may belong to the opposite side of the spine from the striate surface, is smooth or much less striate and bears seta sockets about 1.5 mm. apart. Each socket has a diameter of 0.15 mm. and is surrounded by an elliptical pitted field, the larger diameter measuring 0.8 mm., the smaller 0.4 mm. (Text-fig. 11h). Such pitted or granulate fields are unknown in other fragments. Towards the tip of the spine the striae define indistinct, elongate scales. Near the distal tip, however, the scale-like structure is distinct, each scale carrying a seta socket. Sockets occur even when the scales are not outlined. It is difficult to determine the true nature of this fragment. The scale-like sculpture and seta sockets suggest an arthropod of a size conforming to *Cyrtoctenus*. The association of the spine with a plate having a straight margin might suggest that it is an epimeral process, developed from a tergite. The presence of such a concentration of setae on the spine would suggest rather that it had a tactile function. Somewhat similar sensory organs have been described by Waterston (1957, p. 275, Pl. 2, fig. 7) from the second and third pairs of prosomal appendages of the large Carboniferous eurypterid *Hibbertopterus scouleri*. Until more material is available, however, too much weight cannot be given to this similarity.

The second specimen R.E. 14755 (Pl. IV, fig. 4) shows the curved edge of a plate the surfaces of which exhibit no distinct pattern although knobs are present. The curved edge of the plate is provided with densely arranged thin, apparently soft, hairs, the longest of which measures 2.5 mm. These hairs must have been quite different in their function from the probably rigid setae occupying the sockets of the specimen described above.

(c) *Cyrtoctenus caledonicus* (Salter)

Pl. I, figs. 1-4; Text-fig. 12.

Cycadites caledonicus Salter. 1863, p. 58. 1866, p. 72, fig. 22.

Glyptoscorpius caledonicus Peach. 1882, pp. 518-519, Pl. 29, figs. 18, 18a, 19.

Non

Glyptoscorpius caledonicus Peach. 1882, Pl. 29, fig. 17.

Glyptoscorpius (*Cycadites*) *caledonicus* Peach in Miller. 1887a, p. 84

Glyptoscorpius caledonicus, White, 1927, p. 286.

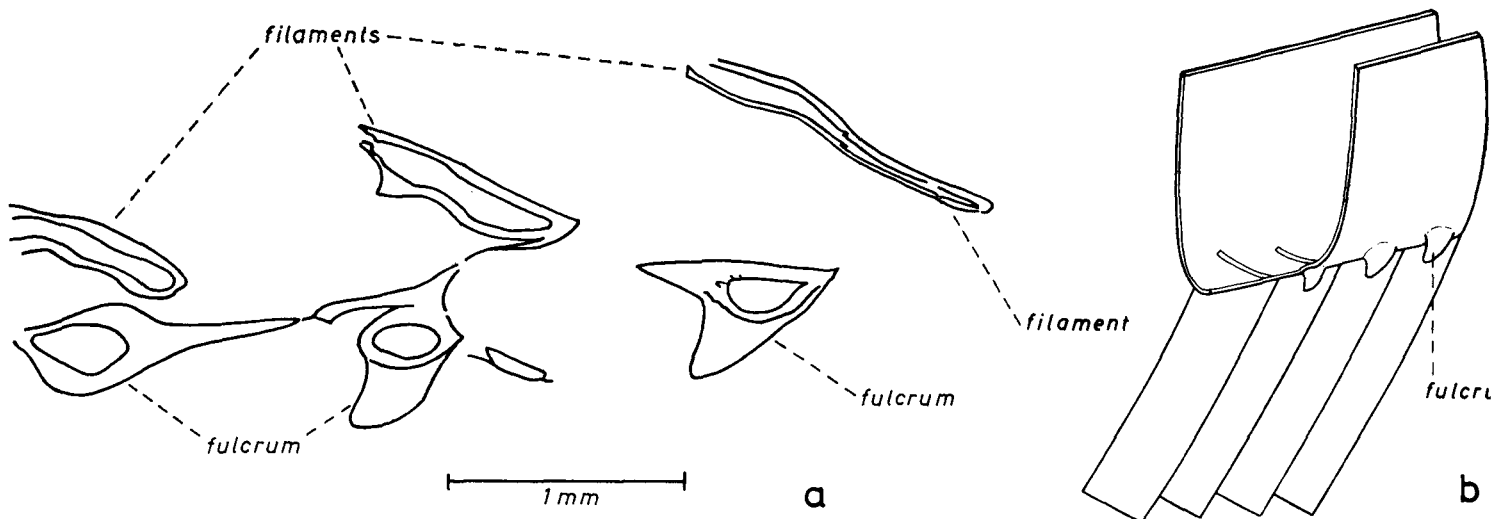
Holotype.—The species is known from the unique holotype G.S.M. 85052 from below the Scremerston Coals in the Cove-Cockburnspath section of the Lower Carboniferous (Viséan) in East Lothian.

Diagnosis.—Appendage B (?) with relatively long filaments and small cone-shaped fulcra spaced at a distance along the rachis exceeding the largest width of the fulcra.

Description

The specimen is plastically preserved in a light coloured sandstone. The fossil parts are black and smooth, sometimes with an uneven surface due to the preservation. A red mineral, possibly haematite, occurs in the internal cavity of the filaments.

A length of 120 mm. of the rachis from the blunt distal tip (Pl. I, fig. 2) is preserved, the distal 20 mm. of which is seen as a mould having a depth of 4.5 mm. and a maximum width of 3 mm. In this part of the appendage the filaments are seen in lateral view but the rest of the shaft is cut off exposing a section across the bases of the filaments. The shaft probably formed a solid structure having a certain thickness, the anterior margin of which



TEXT-FIG. 12.—*Cyrtoctenus caledonicus* (Salter). *a.* cross-section at the base of filaments and fulcra; G.S.M. 85052. *b.* diagram showing position of filament and fulcra at the base of rachis.

was curved and the posterior border but slightly curved. Peach evidently assumed that the rachis possessed two rows of filaments at the posterior margin (Peach 1882, Pl. 29, fig. 18*a*) as in what we now recognize as appendage A of *C. peachi* from Lennel Braes. A closer study of the section along the base of the rachis shows, however, that typical filaments occur on the presumed dorsal side of the shaft only. On the ventral side there are a corresponding number of short, hollow fulcra (Text-fig. 12; Pl. I, figs. 3, 4), probably homologous with the fulcra of appendage B in the type species (Text-fig. 4).

Some 60 to 70 filaments are preserved along the rachis, mostly in section, both transverse and longitudinal, but the surfaces of individual filaments are preserved in places. They are attached to the shaft at an angle of between 30° and 40° opening distally (Pl. I, fig. 1). The more distal filaments form a smaller angle and are bent and twisted to become nearly parallel to the shaft (Pl. I, fig. 2). Each filament is nearly flat with a fairly constant width of about 1 mm. The maximum length observed is 19 mm. The smooth filaments are hollow (Text-fig. 12*a*) and there are no traces of ridges or denticulate edges as in the filaments of appendage A of *C. peachi*. The filaments are gently curved outwards with their concave margin towards the distal end of the shaft, and their ends are blunt, not narrow and pointed, as in appendage A of the type species, but resemble in shape those of appendage B of that species.

The fulcra, occurring on the ventral side of the shaft, are more or less cone-shaped, having blunt ends and elliptical cross-sections. Those cross-sections exposed (Text-fig. 12*a*)

appear to be at the base of the fulcra. Their length is only 0.5 mm., and the largest cross sections at the base are between 0.4 mm. and 0.6 mm. in their longest dimension. The distance between the fulcra is about 0.9 mm. They are situated opposite the filaments.

The shape of the filaments with their lack of denticulate margins, and the presence of conical fulcra instead of filaments on the ventral side of the posterior margin of the rachis, suggest that the specimen represents appendage B, rather than appendage A as was assumed by Peach. The filaments, with a length of 19 mm., are longer than is usually seen in appendage B of the type species in which those of the holotype, a large and possibly old individual, measure only 11.5 mm. in length.

Remarks

The present species differs from *C. peachi* by having small cone-shaped fulcra and longer filaments (if appendage B). The filaments are hollow, not solid as in *C. peachi*. This, however, might possibly be due to the preservation or a secondary fusion in the latter.

(d) *Cyrtoctenus ostraviensis* (Augusta and Pribyl)

(?) *Stylonurus* (*Ctenopterus*) *ostraviensis*. Augusta and Pribyl 1951,
pp. 1–9, Pl. 1, figs. 1, 2.

Mazonipterus (?) *ostraviensis*, Kjellesvig-Waering, 1966, p. 193.

Material.—Known from a unique holotype from the Middle Namurian Ostrava Beds, Petr Bezruč mine, Ostrava, Czechoslovakia.

The fragment described by Augusta and Pribyl (1951) has a length of 65 mm. suggesting that it represents a rather large comb-like appendage. The arc-shaped shaft has a crossing furrow which gives the appearance that it is made up of two segments. The close resemblance of the specimen to appendage A in *Cyrtoctenus peachi* and *C. dewalquei* would suggest, however, that the shaft consists of one segment only. The shaft is covered with plicae. The filaments occur at a number of 8–9 at a length of 10 mm., corresponding to 11 in *C. dewalquei*, and 8–9 in the holotype of *C. peachi*.

C. ostraviensis may belong to *C. peachi*, but as long as the material is so limited, the species may be maintained meanwhile.

IV. THE STRUCTURE AND AFFINITIES OF THE GENUS *CYRTOCTENUS*

Although our knowledge of *Cyrtoctenus* is very limited, we have detailed knowledge of the structures of the abdominal appendages which demonstrate several morphological features which appear to be of general interest in considering the evolution of the Arthropoda and provide some evidence for considering the affinities of this unique arthropod.

Affinities.—The appendages and plates described belonged to a large arthropod. Combs similar to the comb-like structures found in *Cyrtoctenus* are known in fossil and recent members of the Order Scorpionida in which they occur on the post genital somite. Wills (1959, p. 261 and 1960, p. 331) has pointed out, however, that no sensory peg-organs occur on the filaments of the combs here defined as *Cyrtoctenus* (*Glyptoscorpium* auct.) and that therefore they could not have belonged to true scorpions. Another major difference between *Cyrtoctenus* and true scorpions is the presence in the former of four extra pairs of finger-shaped abdominal appendages. In arachnids, including the scorpions, these appendages are

probably transformed into the so-called sternites (Størmer 1963, p. 112). Only in the Xiphosura of the Class Merostomata do the appendages of the somites IX–XIII appear as free movable appendages, while the four posterior pairs have rows of lamellae which may be homologous with the teeth of the scorpionid comb as mentioned below.

On the shafts of the combs and on the associated plates of *Cyrtoctenus* typical eurypterid-type scales have been described, and for this reason we have referred *Cyrtoctenus* with doubt to the Subclass Eurypterida of the Class Merostomata. The eurypterids, however, have no comb-like appendages, the abdominal appendages being plate-shaped. While structures somewhat similar to the filaments of *Cyrtoctenus* are found on the prosomal appendages of certain eurypterids such as *Mixopterus* (Størmer 1934b) and *Megalograptus* (Caster and Kjellesvig-Waering 1955) the prosomal appendages are jointed whereas the filaments occur in *Cyrtoctenus* on a long unjointed rachis.

Other groups of arthropods appear to have little in common with the present genus. We conclude therefore that *Cyrtoctenus* probably belongs to the Subphylum Chelicerata comprising the Classes Merostomata and Arachnida. Among the Chelicerata the Scorpionida and Eurypterida show the closest relations to *Cyrtoctenus*. It may be noted that Dubinin (1959) has recently placed the eurypterids and scorpions in one unit of the Chelicerata. Because of its unique characters the genus *Cyrtoctenus* probably belongs to a new order within the Eurypterida for which we propose the name Order CYRTOCTENIDA.

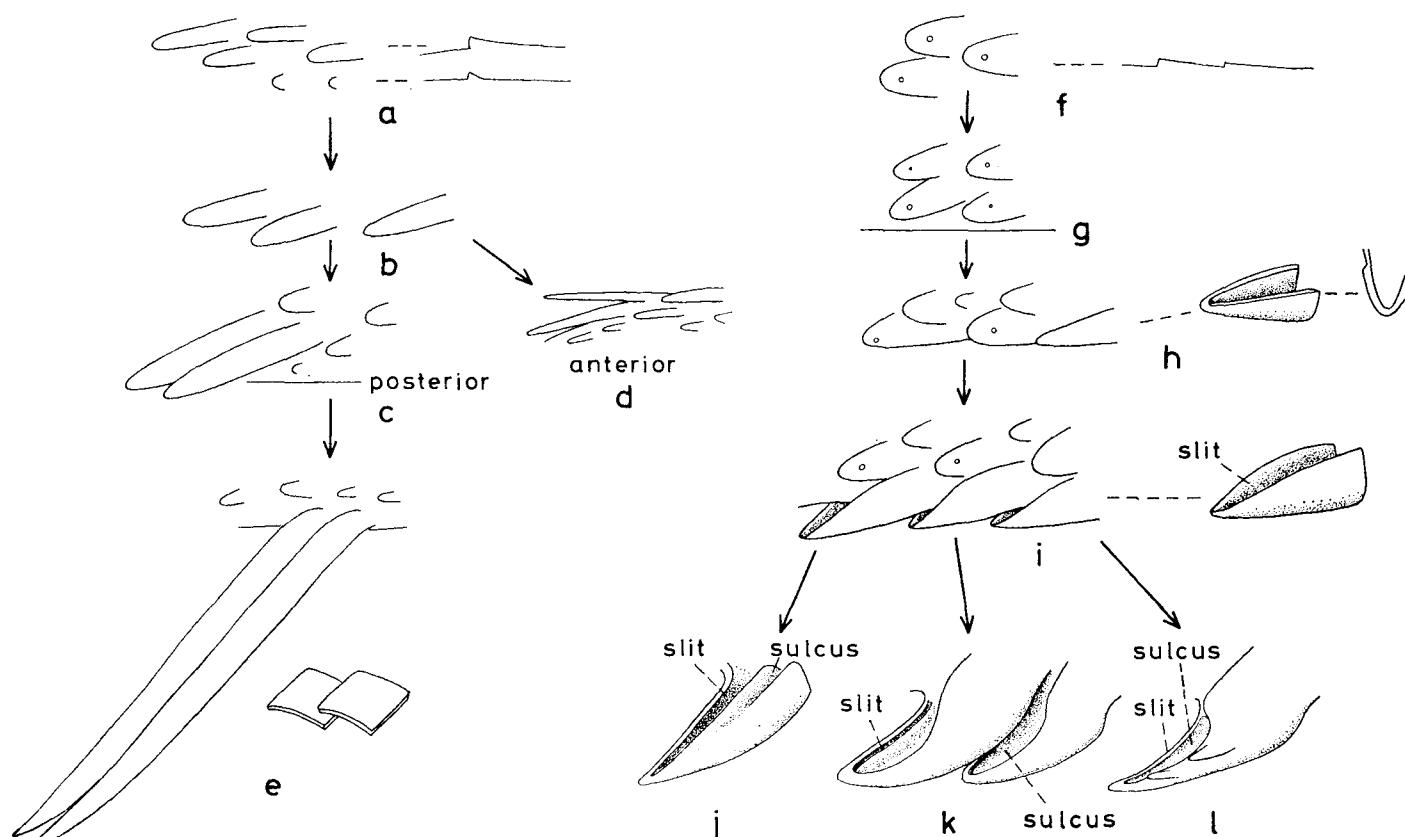
The Structure and Development of Filaments and Fulcra.—The well preserved Scottish material of *Cyrtoctenus peachi* demonstrates rather convincingly the development of the filaments and fulcra from particular types of scales. Although there are transitions between the types of squamation, there are two forms of scale which are characteristic. The first is the elongate flat scale-tubercles with raised distal ends and parallel sides which become obsolete and which show no traces of setae (Text-fig. 13a). The second is the parabolic “eurypterid” type of scales with a steep distal margin and often with setae (Text-fig. 13f).

The filaments evidently develop from the first type. These elongate flat scale-tubercles do not differ much from those found in certain scorpion-like eurypterids such as the Mixopteridae and Carcinosomidae. In *Cyrtoctenus* this ornament occurs on both sides of the rachis of appendage A, which also bears long flat filaments in two rows along the posterior border. A gradual transition from scale-tubercle to filament is not directly demonstrated along the margin. Flat spines, similar to filaments, do develop gradually from scale-tubercles, however, in the more distal portion of the rachis (Text-fig. 13d; Pl. VI, fig. 7). It is significant that in appendage B the dorsal surface only of the rachis has scale-tubercles and only one row of flat filaments is developed in this appendage (Text-figs. 4c, d). Flat spines along the anterior margin have been noted also in appendage D in which the surface of the rachis is smooth and apparently without scale-tubercles (Pl. VI, fig. 8).

The fulcra are associated with scales of the eurypterid type and in this case it has been possible to follow the transition step by step from scale to fulcrum as the structures are traced from the proximal to the distal portions of the finger-shaped appendages. The transition has been demonstrated in appendages B, D and E (Text-figs. 4, 6 and 7).

In the basal portion of the rachis the distally directed parabolic scales (Text-fig. 13f) have a more postero-distal direction near the posterior margin (Text-fig. 13g). At the margin the scales are bent along the median line, leaving one half on the ventral side and one half on the dorsal side of the rachis (Text-fig. 13h). The two halves may be unequal with the larger part on the ventral or dorsal side. The next stage in the development of the marginal scales is characterized by a postero-distal prolongation of the tip of the scales (Text-fig. 13i)

which is the beginning of the formation of the marginal spines or fulcra. The enveloping scale forming the initial fulcrum (Text-fig. 13i) has an anterior opening occupying the space between the two halves of the scale, and the scale distal to it. In a further stage of development this opening or slit may remain open almost to the tip (Text-fig. 13j) or both margins of the scale may approach one another in the distal part so that the slit becomes more or less closed (Text-figs. 13k, l). These structures are generally complicated, however, by a sigmoidal furrow or sulcus (Text-figs. 13j-l). The primary opening or suture may run outside



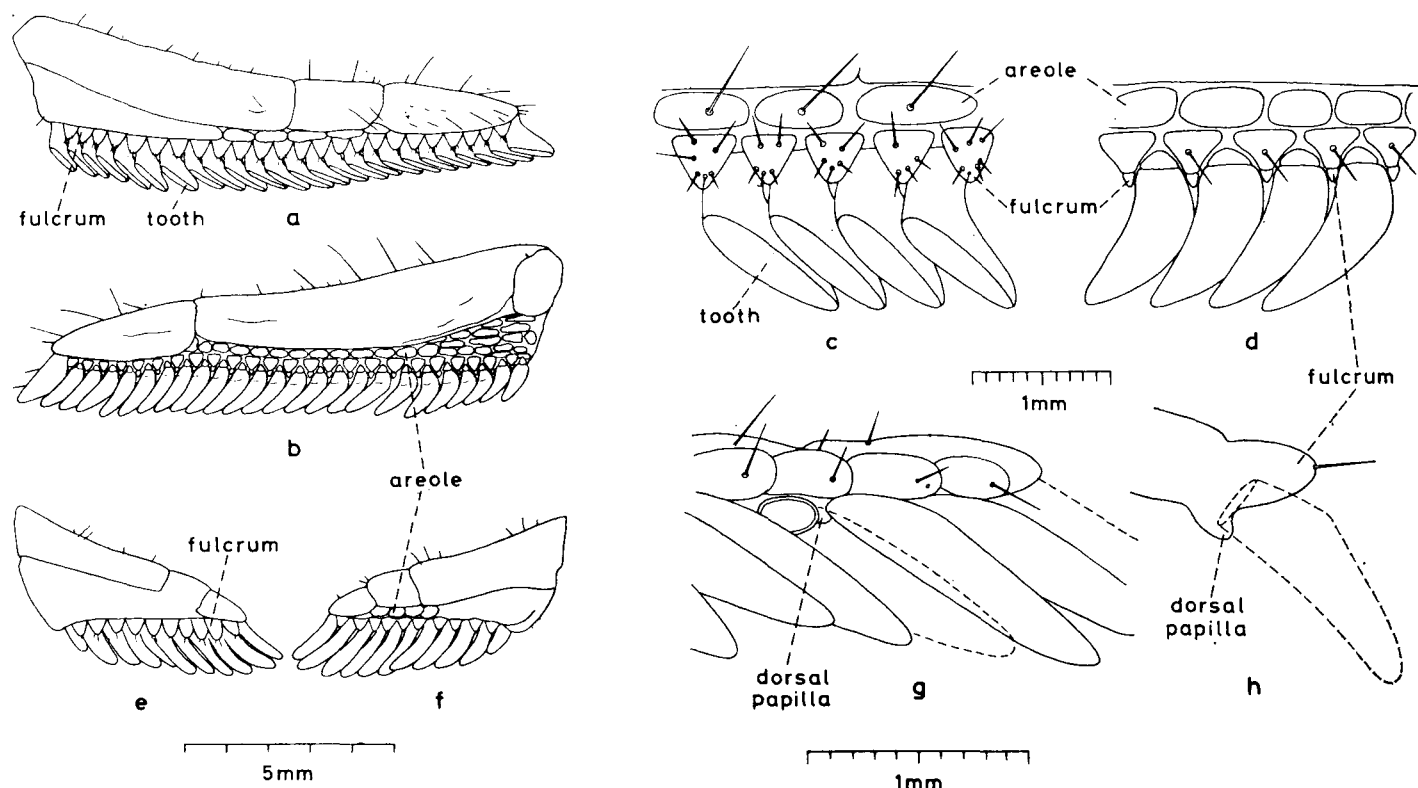
TEXT-FIG. 13.—Diagrams showing the probable development of filaments and fulcra from two different types of scales (or scale-tubercles). *a-e*. Development of filaments from tongue-shaped scale-tubercles; *f-l*. development of fulcra from eurypterid type scales. The various samples are mostly taken from diagrams presented in Text-figs. 3-7.

the sulcus (Text-fig. 13j) or occur at the border of the sulcus (Text-fig. 13k), or be situated on the distal wall between the dorsal and ventral surfaces (Text-fig. 13l). Since the fulcra are rather close set, the sulcus may have served as a bed for the fulcrum distal to it (Text-figs. 13k, l), the proximal margin of the distal fulcrum fitting into the sulcus near, or at, the distal margin of the fulcrum proximal to it. This may have been useful when the rachis was bent or twisted. A further elaboration of the fulcra takes place by the development of internal ridges and septa and external ridges and rims (Text-figs. 4g, h; Text-figs. 7d-g, h).

The tendency to form minute rows of small teeth is also characteristic in *Cyrtoctenus*. Rows of short spines are found on the filaments both in appendages A and B (Text-figs. 3b-d, f; 4e). They also occur on the more specialized fulcra in appendages B and E (Text-figs. 4h, i; 7e, g, k).

The phylogenetic significance of the structures.—As in *Cyrtoctenus* fulcra are developed from eurypterid-like scales and filaments from elongate scale-tubercles, so in the Carboniferous scorpion *Gigantoscopus* there is a tendency to form fulcra from scales and possibly

also the filament-like teeth similarly (Størmer 1963, Text-fig. 20). In this genus the surface of the pecten is covered by rounded scales or flat tubercles, termed areoles in scorpion literature, and the fulcra may be interpreted as a specialization of the areoles or plicae along the posterior margin of the pecten (Størmer 1963, p. 57). In *Gigantoscrapio* there are more than sixty flat sabre-shaped teeth along the posterior margin of the pecten. Whether they comprise one or two rows is uncertain, but the former seems the more probable. These



TEXT-FIG. 14.—Pectines of Recent scorpions from South Africa. *a, b.* ventral and dorsal surface of pectine of *Hadogenes trigolytes*; *c, d.* details of areoles, fulcra and teeth of the same, ventral and dorsal view; *e, f.* ventral and dorsal view of pecten of *Pandinus viatorus*; *g.* posterior view of teeth (one removed and distal one lacking) and fulcra, and dorsal papilla; *h.* diagrammatic section showing fulcrum and dorsal papilla, tooth stippled.

teeth are thus not very different from the filaments in appendages A and B in *Cyrtoctenus*. We do not know, however, whether or not the fulcra in *Gigantoscrapio* were intercalated as fixed plates between the bases of the filaments, or had a free exposed part as in *Cyrtoctenus*.

In order to study the structures of the fulcra in Recent scorpions certain South African species, kindly sent to the senior author by Dr. P. F. Lawrence, Natal, have been examined. Text-fig. 14 shows the pectines of two larger scorpions, *Hadogenes trigolytes* and *Pandinus viatorus* (total length of body 189 mm. and 100 mm.). In *Hadogenes* (Text-figs. 14*a, b*) the rachis is divided by crossing furrows into three pieces on the ventral surface, but only in two pieces on the dorsal side. Of particular interest is the development of the areoles corresponding to the scales in *Cyrtoctenus*. On the ventral surface (Text-fig. 14*a*) the areoles are less distinct, but on the dorsal surface (Text-fig. 14*b*) they occupy the total surface of the middle lamella and occur even at the base of the teeth between the fulcra (Text-fig. 14*d*). The areoles appear as slightly convex papillae, usually with an elliptical outline, and they occur in up to five rows in front of the fulcra. The areoles are similar to those found in the

Carboniferous *Gigantoscrapio* and are probably homologous also with the scales in *Cyrtoctenus*. The triangular fulcra in *Hadogenes* are provided with more setae than are the corresponding plates on the dorsal side of the pecten.

In *Pandinus* in particular (Text-figs. 14e-g) the position of the teeth indicates a considerable mobility of these structures for when the teeth are bent in a dorsal direction the fulcra maintain their posterior direction. The teeth and the fulcra do not form one solid unit which might indicate that the fulcra developed from marginal ventral scales or areoles, while the teeth developed from dorsal ones, as has been demonstrated in *Cyrtoctenus*.

A comparison of the comb-structures in *Cyrtoctenus*, *Gigantoscrapio* and in Recent scorpions makes it very probable that these structures are homologous and that the teeth and fulcra developed from the integumental scales.

Do we find similar structures in other arthropod groups? Among the arachnids pectines are confined to the scorpions, but, as pointed out by Lankester (1881a, b), the lung-books of scorpions and certain other arachnids developed from external appendages which, during embryological development, sink within the body. The combs and lung-books in arachnids are therefore evidently homologous with the abdominal appendages bearing book-gills in *Limulus*. As one of us has noted the abdominal appendages in *Limulus* are probably homologous with the gill-branch of the appendages in trilobites and certain other forms belonging to the Trilobitomorpha (Størmer 1939, 1944).

When we consider the phylogenetic significance of the structures in *Cyrtoctenus*, three alternatives appear possible:

1. The comb-like structure might have developed independently in different arthropod groups, their similarity being a case of homeomorphy only.
2. The structure expresses an evolutionary tendency characteristic of a major arthropod stem (the Arachnomorpha).
3. The comb-like structures are homologous representing an evolutionary link between the Trilobitomorpha and the Chelicerata.

Since the fulcra and teeth or filaments evidently develop directly from scales and areoles one might assume that this could happen in very different groups. However, the presence of typical eurypterid scales in *Cyrtoctenus* indicates that this genus probably belongs to the same major group as the eurypterids, the Chelicerata. Could these comb-like structures develop independently within the Chelicerata? It is possible, the structures are so specific that they at least would represent an evolutionary tendency within the Chelicerata as postulated in the second alternative. It is important to notice that the pectines remained after the scorpions changed from an aquatic to a terrestrial mode of life. This profound change in habitat probably changed the function of the pectines also. Since comb-like appendages also appear to be characteristic of the Trilobitomorpha, the tendency must also embrace this major group.

The occurrence of comb-like structures both in the Chelicerata and the Trilobitomorpha suggest a common tendency within members of these groups to form such structures. However, since the structures are so complicated (their nature has not been fully ascertained in the early Palaeozoic Trilobitomorpha), the occurrence in common of such structures might provide evidence for more than a tendency and be rather an expression of mutual relationship.

The present considerations suggest that the comb-like structures in the various groups of Chelicerata and Trilobitomorpha express a common evolutionary tendency among their members, and it is very possible that the structures are homologous, indicating a relationship between members of these groups.

Habitat.—With our very imperfect knowledge of *Cyrtoctenus* it is difficult to reconstruct its mode of life. Because of its large size it must almost certainly have been aquatic since such a heavy body could hardly have been supported by the prosomal appendages on land. The facies in which its remains are found would also suggest that the animal belonged to the estuaries as did the contemporaneous giant scorpion *Gigantoscrapio* which, it has been suggested, may have been able to spend short periods on land (Størmer 1963, pp. 122–134).

It is possible only to guess at what the functions of the abdominal appendages might have been. Since the filaments of the comb appendage are devoid of peg-organs, and the shaft does not appear to possess many distinct sensory hairs, the cyrtoctenid appendage A would not appear to have served as a tactile or sense organ. In the other appendages, particularly B and E, the scales had setae which may have served a sensory function. The abdominal appendages were probably the most heavily chitinized structures of *Cyrtoctenus* since it is these appendages which are found almost to the exclusion of all else. The thick cuticula of the appendages, therefore, would appear to rule out a respiratory function for them such as is the case in the laminae of the book-gills on the abdominal appendages of *Limulus*.

The flat finger-shaped shafts, with or without filaments, may have served as a protection for the gills which, as in eurypterids (Wills 1965), may have been situated on the ventral body wall or on special extensions to it. They may also have served for swimming, but more probably as stabilizing fins (see Størmer 1963, p. 96 for a discussion of the function of the combs in *Gigantoscrapio*). While these suggestions are probable, the highly specialized nature of the abdominal appendages, with their development of filaments, fulcra, teeth and barbs, would suggest that they may also have been used for a more specialized function, the nature of which must remain a matter of speculation. Did the barbs serve as an aid for filtering the water for animalculi subsequently transferred from the combs to the mouth in nutrition (for a discussion of the possible filtration function of trilobite limbs see Størmer 1939, p. 227), or did they serve as an aid for attachment of the eggs to facilitate their oxygenation as in modern crustacea?

V. DISTRIBUTION OF *CYRTOCTENUS*

The Devonian flags of Pont-de-Bonne-Modave in the Belgian province of Liège, from which *Cyrtoctenus dewalquei* was obtained, were assigned to the Assise d'Evieux of the Upper Famennian by Murlon (1902) and to stage Fa 2c by Stockmans (1948). The fauna associated with *C. dewalquei* includes the eurypterid *Adelophthalmus* (?) *lohesti* (Dewalque) (see Kjellesvig-Waering 1958, p. 1141), and the fishes *Phyllolepis undulata* Lohest, *Holoptychius flemingi* Ag. (= *H. dewalque* Lohest) and teeth of *Holoptychius* (see Leriche 1931). The following plants are recorded by Stockmans (1948) *Archaeopteris roemeriana* (Göppert), *Sphenopteris modavensis* Stockmans and *Rhacopteris condrusorum* Crépin. The flora indicates the proximity of land from which the plants were derived and the fauna is of a non-marine aspect. In his original description Fraipont (1889) records the presence of *Lingula*. It seems unlikely that, if this fossil occurs at Pont-de-Bonne, it was obtained from the same bed as that yielding the fish and eurypterid fauna. Although parts of the fauna, like the flora, would have been derived, it seems unlikely that the delicate structures of the well preserved *Cyrtoctenus* combs could have travelled far.

Cyrtoctenus peachi occurs in Britain in strata of the Cementstone Group in Northumberland, Berwickshire and East Lothian, but unfortunately it is not yet possible to zone this

rock unit which may lie in the Lower Viséan and/or Upper Tournaisian (Garwood 1931, Trotter and Hollingworth 1932, George 1958, Lumsden *et al.* 1967). A specimen referred with hesitation to the species comes from the Glencartholm Volcanic Beds at the base of the Upper Border Group which has been assigned to a C_2S_1 to S_2 age (Lumsden and Wilson 1961, Lumsden *et al.* 1967) while a proved specimen of the species bears the locality "Tarras Waterfoot, Eskdale".

A striking feature about the occurrence of *C. peachi* is its frequent association with the type of vertebrate fauna first described from the Crooked Burn, Foulenden, Berwickshire (White 1927). Here a characteristic suite of palaeoniscid fish occurs of which six forms are now recognized—*Styracopterus ottadinicus* (White), *Carboveles ovensi* White, *Aetheretmon valentiacum* White, *A. valentiacum* var. *ovensi* White, *A. whitei* Moy-Thomas and *Strepheoschema foulendenensis* White. Associated fossils include *Acanthodes ovensi* White, sharks, lamellibranchs and arthropods which, in addition to *C. peachi* (Pl. III, fig. 11) include *Crangopsis eskdalensis* and *Tealliocaris* sp.. Moy-Thomas (1938) re-examined the palaeoniscids from the Coomsdon Burn, Northumberland, which had been obtained from grey sandy shale half a mile above its junction with the River Rede, the fauna of which was recorded by Miller (1887, pp. 83–84), and found that four forms, *Styracopterus ottadinicus* (White), *Aetheretmon valentiacum* White, *A. valentiacum* var. *ovensi* White and *Strepheoschema foulendenensis* White were the same as those occurring at Foulenden while the remaining two, *Aetheretmon whitei* var. *rhodesi* Moy-Thomas and *Strepheoschema rhodesi* Moy-Thomas were closely comparable with Foulenden forms, while shark remains are also found. Coomsdon has also yielded *C. peachi*, scorpions, crustacea and a xiphosuran, in addition to brachiopods, lamellibranchs, gasteropods and cephalopods.

Moy-Thomas compared the Foulenden fauna also with that of two other localities from which *C. peachi* has been obtained, the River Tweed below Coldstream Bridge in Berwickshire and Tarras Waterfoot, $2\frac{1}{2}$ miles S.S.E. of Langholm, in the burn just below the railway (see Westoll in Watson, Westoll, White and Toombs 1948, p. 15). *Styracopterus ischipterus* (Traquair) occurs at the former locality, which being a juvenile form may prove to be synonymous with *S. ottadinicus* (Moy-Thomas 1938, p. 317), while at the latter locality Moy-Thomas reports the occurrence of *Styracopterus fulcratus* Traquair and *Rhadinichthys laevis* Traquair. As described below special difficulties attach to the Tarras Waterfoot locality, but although the evidence is weaker for Coldstream Bridge, the presence of this unusual palaeoniscid, together with *C. peachi*, makes it reasonable to suppose a possible equivalence of these faunas with those of Foulenden and Coomsdon Burn.

We are grateful to Dr. R. B. Wilson (personal communication) for drawing our attention to the possible confusion of the Tarras Waterfoot locality with that of Glencartholm which lies a quarter of a mile above Glencartholm in the River Esk, some four miles south of Langholm, Dumfriesshire (Westoll in Watson *et al.* 1948, p. 15). This may have arisen through the description of the locality in his collector's register by the pioneer Geological Survey collector A. Macconochie as "River Esk, Glencartholm, Langholm at Foot of Tarras Water, 3 m. S. of Langholm". It may well be, therefore, that fossils stated to have come from Tarras Waterfoot have in fact been collected at Glencartholm. It is known that Jex and Stock collected in Eskdale but there is little evidence in their collections that they distinguished between Tarras Waterfoot and Glencartholm. Moy-Thomas collected extensively in Eskdale, but through the kindness of Mr. H. A. Toombs of the Palaeontological Department of the British Museum (Nat. Hist.), who has checked his material and correspondence between 1933 and 1938, we can say that although Moy-Thomas writes about

visiting Glencartholm most years, Tarras Waterfoot is not mentioned, nor does that locality appear in his material. We are forced to conclude, therefore, that it is possible that although *C. peachi*, *Styracopterus fulcratus* and *Rhadinichthys laevis* are reported to have been found at Tarras Waterfoot, a fauna that would accord well with that of Foulden, Coomsdon Burn and Coldstream Bridge, these fossils may have been obtained from the Glencartholm Volcanic Beds.

The associated fossils from the Tuedian localities would suggest that *C. peachi* lived in estuarine conditions. The proximity of land is indicated by the presence of plant remains, but members of the fauna more associated with marine conditions are the sharks and, particularly in the case of the Coomsdon Burn, the presence of brachiopods, gasteropods and cephalopods would indicate a stronger marine influence. The fossils from Glencartholm were obtained from a calcareous shale in the Glencartholm Volcanic Beds and include plants, ostracods, brachiopods, lamellibranchs, cephalopods, crustaceans, scorpions, eurypterids and fishes. The faunal list is given by Peach and Horne who state (1903, p. 845) that the scorpions and plants usually occur together in a separate bed, while crustaceans are found in association with the fishes which are themselves usually found underneath a band in which *Orthoceras* is a conspicuous fossil. *Spirorbis* and adherent brachiopods are found attached to plant stems and some bands of the shale are covered with the chitinous tubes of marine worms. It was the view of Peach and Horne that the shales containing the organic remains may have been deposited in a muddy creek, shut off at intervals from the open sea. Although true marine limestones occur above the Glencartholm beds, the calcareous shales could not have been deposited in the open seas since the contained fossils are of "estuarine" aspect and would indicate the presence of a nearby shoreline. Basic tuffs occur above and below the fossiliferous shales, however, and while a nearby shoreline is evident, it remains open to question whether the shales were deposited in brackish estuarine conditions, or whether the presence of volcanic ash in the water has inhibited the development of a more truly marine type of fauna (Lumsden *et al.* 1967, p. 108).

Peach (1882, p. 522, Pl. XXIX, fig. 21) described and figured a specimen, probably of *Cyrtoctenus* found by Thomas Stock in the Tweeden Burn, Liddesdale. Unfortunately this specimen has not been traced and since no exact location within the Tweeden section is given it is not possible to tell from what horizon the specimen was obtained.

C. caledonicus (Salter) is stated to have been found in "a hard micaceous sandstone at the base of the Carboniferous rocks, or rather at the base of that portion of them which immediately overlies the red and yellow sandstones of Berwickshire. It occurs at Cockburnspath a few miles S.E. of Dunbar, and in beds which contain a large *Sigillaria*, *Lepidodendron*, fish defences (*Gyracanthus*) and a few Carboniferous shells" (Salter 1863, p. 58). The provenance is too incomplete to be sure from which bed in the Carboniferous succession east of Cove, East Lothian, the specimen was obtained, but it probably came from below the outcrop of the Scremerston Coals (see Clough *et al.* 1910, p. 44) since in a later paper Salter (1866, p. 73) says that the specimen came from "a bed below the coal beds of Cockburnspath Cove". A good D₁ fauna, including goniatites, was obtained from the Cove Lower Marine Band (H. H. Wilson 1952) which Wilson correlated with the Dun Limestone of Berwick and the Redesdale Ironstone. Beds below the Scremerston Coals must therefore probably lie in S₂ and fall within the lower middle Viséan. The coarseness of the sandstone would suggest that the comb and the associated plant remains must have been transported to the area of deposition.

In their description of *C. ostraviensis* Augusta and Pribyl (1951, pp. 7–8) state that the

specimen was found in the Ostrava Beds, in the Hrušov Zone, in the Marine horizon X of Františka of the Namurian A in Czechoslovakia. A marine fauna of lamellibranchs, gasteropods and a trilobite is found in association with *C. ostraviensis*.

With the exception of the Czechoslovakian Namurian occurrence, *Cyrtoctenus* is found in non-marine or estuarine environments associated with conditions existing during, or immediately prior to, the Carboniferous marine transgression over the Old Red Sandstone North-European continent. It may well be that the widespread marine conditions existing in the mid-Carboniferous proved unfavourable to this genus, which was apparently specialized for life in estuarine conditions, and so contributed to its early extinction.

VI. PROBABLE SAPROPHYTES ON *CYROTOCTENUS*

1. *Microorganisms*.—In one of the smaller specimens of *Cyrtoctenus peachi* (G.S.E. 2127 from Lennel Braes, Berwickshire) the chitinous integument is very little altered. Parts of the skin, particularly the filaments of appendage A, were peeled off and bleached with Schulze's solution (potassium chlorate and concentrated nitric acid), and afterwards embedded in Canada Balsam, the same procedure that was used for *Gigantoscorpio* (Størmer 1963, p. 113).

The microfossils are apparently similar to those described by Moore (1963) in *Gigantoscorpio*, and the material may be described by Professor Moore later. A few samples of the microfossils are shown in Pl. II, figs. 3–6, and Pl. IV, fig. 13. They probably belong to the "spherical or ellipsoidal bodies" described by Moore (1963, p. 9; Pl. II, figs. 2, 4–6). The minute granules or cocci are visible inside the large body (Pl. II, figs. 3–5). One specimen (Pl. II, fig. 6) shows what appears to be some kind of a string attachment. This body also demonstrates the beaded and apparently ramifying tubules described by Moore. In another specimen (Pl. IV, fig. 13) the spherical body seems to have been resolved, releasing the beaded tubules which are very distinct.

The microorganisms described probably attacked the skin after the *Cyrtoctenus* specimen had died (or the microorganisms might have attacked the empty exuviae after moulting).

2. *Spirula-like organisms*.—A Belgian specimen (R.E. 14783A), representing appendage E of *Cyrtoctenus dewalquei*, shows numerous impressions of *Spirula*-like specimens on the skin (Pl. III, fig. 19; Pl. VI, fig. 15). The specimens, which seem to be attached to the outside of the skin, have a diameter of from 0.5 mm. to 1.5 mm. Only two whorls are visible. It is possible that the *Spirula*-like organisms were already attached to the integument of the host during life.

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IX. DESCRIPTION OF PLATES

Photographs not retouched

PLATE I

Figs. 1-4,

Cyrtoctenus caledonicus (Salter), Holotype G.S.M. 85052, Calciferous Sandstone Measures, Cockburnspath, East Lothian.

- Fig. 1. Appendage B in dorsal view. $\times 1.3$.
 Fig. 2. Distal portion of the same. $\times 3.7$.
 Fig. 3. Exposed cross section of bases of fulcra and filaments. $\times 10$.
 Fig. 4. As above.

Figs. 5-17,

Cyrtoctenus peachi n. sp.

With the exception of Fig. 9, Figs. 5-17 represent the Holotype, from the Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire.

- Fig. 5. Rachis of appendage A with well developed elongate scale-tubercles near the anterior margin, G.S.E. 2184. $\times 1.1$.
 Fig. 6. The three appendages A, B, and C in dorsal view, G.S.E. 2185. $\times 0.8$.
 Fig. 7. Appendages A, B and D in ventral view, G.S.E. 2184. $\times 0.8$.

Fig. 8. Posterior margin of appendage B with filaments. Dorsal view with impressions of scales on the ventral surface of the rachis, G.S.E. 2185. $\times 3.4$.

Fig. 9. Elongate tubercles on the rachis of appendage A. G.S.E. 5864(8), Cementstone Group, River Tweed, Coldstream Bridge, Berwickshire. $\times 7$.

Fig. 10. Elongate tubercles on the dorsal surface of the rachis of appendage C, G.S.E. 2184 (11). $\times 7$.

Fig. 11. Tubercles on the dorsal surface of the rachis of appendage B, G.S.E. 2184 (4). $\times 7$.

Fig. 12. An isolated piece of appendage B showing the scales and fulcra at the posterior margin of the rachis in ventral view, G.S.E. 2184 (3). $\times 10$.

Fig. 13. The same isolated piece of appendage B as figured in 12, showing the basal portion of a filament and the inside of two fulcra in dorsal view, G.S.E. 2184 (3). $\times 10$.

Fig. 14. Ventral (inner) surface of the filament shown in Fig. 13, G.S.E. 2184 (3). $\times 10$.

Fig. 15. An isolated filament of appendage B, G.S.E. 2184 (6). $\times 10$.

Fig. 16. Rachis of appendage B with fulcra. The fulcra shown in Fig. 12 are the second and third from the left in this figure, G.S.E. 2184. $\times 2.6$.

Fig. 17. The same as in Fig. 16 after the piece shown in Figs. 12 and 13 has been removed. The filaments belonging to the dorsal surface are exposed, G.S.E. 2184. $\times 2.6$.

PLATE II

Cyrtoctenus peachi n. sp.

Figs. 1–18 represent specimens from the Cementstone Group of Lennel Braes, Tweedmill, Coldstream, Berwickshire.

Fig. 1. Impressions of scales on the ventral surface of appendage C, Holotype G.S.E. 2185. $\times 2.2$.

Fig. 2. Scales on the ventral surface of appendage D, Holotype G.S.E. 2184. $\times 2.2$.

Fig. 3. Microorganism on the cuticula of a filament of appendage B, Holotype G.S.E. 2184. $\times 87$.

Fig. 4. Detail of organism shown in Fig. 3. $\times 350$.

Fig. 5. Detail of organism shown in Fig. 3. $\times 350$.

Fig. 6. Microorganism on the rachis of appendage B, G.S.E. 2127 (6). $\times 350$.

Fig. 7. Rachis with fulcra of appendage B, Holotype G.S.E. 2186. $\times 2.9$.

Fig. 8. Distal portion of fulcrum removed from appendage B seen in ventral view, Holotype, G.S.E. 2186 (1) $\times 4.6$.

Fig. 9. Fulcrum shown in Fig. 8 seen in dorsal view. $\times 4.6$.

Fig. 10. Details of fulcra shown in Fig. 7. $\times 5.8$.

Fig. 11. Appendage E, G.S.E. 9682. $\times 1.4$.

Fig. 12. Detail of appendage E as shown in Fig. 11 (whitened). $\times 2.3$.

Fig. 13. Fulcra removed from posterior margin at the mid-point of appendage E shown in Fig. 11, seen in ventral view. One fulcrum is separated from its neighbour. $\times 13.6$.

Fig. 14. The same in lateral view showing concealed teeth. $\times 13.6$.

Fig. 15. The same in dorsal view with the teeth partially visible. $\times 13.6$.

Fig. 16. Tubercles on dorsal (?) surface near posterior margin of appendage B, Holotype G.S.E. 2186 (2). $\times 7$.

Fig. 17. Distal portions of appendages A and B. The ventral cuticula of the most distal portion of appendage B is dislocated, G.S.E. 2127. $\times 2.7$.

Fig. 18. Appendages A and B, G.S.E. 2127. $\times 1.3$.

PLATE III

Figs. 1–18,

Cyrtoctenus peachi n. sp.

Fig. 1. Basal portion of appendages A and B, G.S.E. 2127, Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 2.1$.

Fig. 2. Appendage A, G.S.E. 2183, Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 1.1$.

Fig. 3. Detail of rachis and basal portion of lower filaments showing the elongate tubercles on the rachis of specimen shown in Fig. 2. $\times 3.3$.

Fig. 4. Detail of distal portion of filaments of specimen shown in Fig. 2. $\times 3.3$.

Fig. 5. Detail of filaments of appendage A. Outer surface of upper filament and inner surface of one lower filament, G.S.E. 2144, Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 7.8$.

Fig. 6. Eurypterid-type scales on a plate, probably a tergite associated with specimen shown in Fig. 2. $\times 3.6$.

Fig. 7. Attachment of filaments to rachis in appendage A, G.S.E. 5864, Cementstone Group, River Tweed, Coldstream Bridge, Berwickshire. $\times 4.9$.

Fig. 8. Attachment of filaments to rachis in appendage A in specimen shown in Fig. 2. $\times 3.3$.

Fig. 9. Overlapping filaments seen from the outside in appendage A showing the longitudinal narrow ridge near the serrate border, G.S.E. 2144, Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 17$.

Fig. 10. A filament of appendage A seen from outside showing ridge and marginal teeth, specimen as in Fig. 9.

Fig. 11. An incomplete appendage A, B.M. (N.H.) In 25982, Cementstone Group, Crooked Burn, Foulden, Berwickshire. $\times 0.7$.

Fig. 12. Filament of appendage A viewed from outside showing the flat outer surface having become secondarily concave, the submarginal ridge and the marginal teeth directed inwards in lateral view, G.S.E. 2144 (2), Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 13.3$.

Fig. 13. Two succeeding filaments of appendage A seen from outside, G.S.E. 5864 (11), River Tweed, Coldstream Bridge, Berwickshire. $\times 7$.

Fig. 14 & 15. The same filaments as shown in Fig. 13, separated and seen from the inside. The opening into the hollow filament is shown at the top and the ventral ridge is seen to become serrate as it moves towards the margin. G.S.E. 5864(11). $\times 7$.

Fig. 16. Another filament from the same specimen seen from the inside. The serrate ridge is seen to become marginal, G.S.E. 5864(10). $\times 7$.

Fig. 17. Segment of a prosomal appendage probably belonging to *Cyrtoctenus peachi* n. sp., G.S.E. 2180, Glencartholm Volcanic Beds, River Esk, Glencartholm, Langholm, Dumfriesshire. $\times 2.2$.

Fig. 18. A piece of integument associated with the specimen shown in Figs. 7, 13–16, possibly representing an intersegmental membrane of *Cyrtoctenus peachi* n. sp., G.S.E. 5864(9). $\times 87$.

Figs. 19–21, —

Cyrtoctenus dewalquei (Fraipont) Assise d'Evieux. Pont-de-Bonne-Modave, Liège, Belgium.

Fig. 19. Appendage E, R.E. 14783A. $\times 1.3$.

Fig. 20. Distal portion of appendage D, R.E. 14731B. $\times 1.2$.

Fig. 21. Counterpart of specimen shown in Fig. 20, R.E. 14731A. $\times 1.2$.

PLATE IV

Figs. 1–12,

Cyrtoctenus dewalquei (Fraipont) Assise d'Evieux. Pont-de-Bonne-Modave, Liège, Belgium.

Fig. 1. Appendage A, R.E. 14786A. $\times 1.1$.

Fig. 2. Counterpart of specimen shown in Fig. 1, R.E. 14786B. $\times 1.1$.

Fig. 3. Possibly a lateral prolongation of the segment of a prosomal appendage, R.E. 14728A. $\times 2$.

Fig. 4. Plate with marginal hairs, R.E. 14755A. $\times 2$.

Fig. 5. Plate exhibiting tongue-shaped tubercles of inverted keyhole type, R.E. 14744. $\times 2$.

Fig. 6. Plate exhibiting scattered circular tubercles, R.E. 14776B. $\times 2$.

Fig. 7. Ornamentation of eurypterid type showing transverse scales changing posteriorly into narrow pointed mucrones, R.E. 14742. $\times 2$.

Fig. 8. Large plate, probably a tergite, exhibiting an ornament of knobs or indistinct scales, R.E. 14770A. $\times 0.5$.

Fig. 9. Large plate, probably a tergite, with a few keyhole-shaped scale-tubercles indicating that the figure has been inverted, R.E. 14777A. $\times 0.5$.

Fig. 10. Eurypterid type ornament, R.E. 14739. $\times 1.2$.

Fig. 11. Plate showing mucronate ornament, R.E. 14735. $\times 2.7$.

Fig. 12. Plate ornamented with oblong tubercles, probably a tergite, in which the doublure is exposed at the posterior margin, R.E. 14760A. $\times 1$.

Fig. 13. Microorganisms on rachis of appendage B, G.S.E. 2127(6), Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 700$.

PLATE V

Figs. 1–11, *Cyrtoctenus peachi* n. sp.

With the exception of Figs. 2–3, specimens are from the Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire.

Fig. 1. Impression of appendage C, Holotype G.S.E. 2185. $\times 0.7$.

Figs. 2–3. Pieces of appendage B showing intra-marginal denticles on ventral (inner) surface of filaments

and part of dorsal surface of rachis with elongate scale-tubercles. G.S.E. 2183(11), River Tweed, Coldstream Bridge, Berwickshire. $\times 8$.

Fig. 4. Detail of appendage B in dorsal view. Filaments are attached to the sculptured rachis, Holotype G.S.E. 2185.

Fig. 5. The holotype showing appendages A, B and D, G.S.E. 2184. $\times 1$.

Fig. 6. The sculpture of the dorsal surface of the rachis of appendage E, G.S.E. 9682(9). $\times 6.7$.

Fig. 7. The sculpture of the ventral surface of the rachis of appendage E showing how the fulcra envelope the posterior margin, specimen as in Fig. 6. $\times 6.7$.

Fig. 8. Fulcra of appendage D in ventral view (shown near the right border in Fig. 5). To the left, part of the ornament of the ventral surface of the rachis is seen, while further to the right an impression of the dorsal surface is exposed. Holotype, G.S.E. 2184. $\times 6.7$.

Fig. 9. Distal portion of a fulcrum isolated from appendage D (the one to right in Fig. 8), seen in dorsal view, Holotype, G.S.E. 2184(12). $\times 6.7$.

Fig. 10. The same in ventral view. $\times 6.7$.

Fig. 11. Serrate margin of a segment of a prosomal appendage (?), Holotype, G.S.E. 2185. $\times 2.5$.

Figs. 12–19, *Cyrtoctenus dewalquei* (Fraipont) Assise d'Evieux, Pont-de-Bonne-Modave, Liège, Belgium.

Fig. 12. Moulds of seta-sockets on plate possibly belonging to segment of prosomal appendage (See Pl. IV, fig. 3), R.E. 14728A. $\times 13$.

Fig. 13. Sculpture of the distal portion of the same plate, R.E. 14728A. $\times 6.7$.

Fig. 14. Appendage A, rachis with two rows of filaments, R.E. 14786A. $\times 6.7$.

Figs. 15–19. Latex impressions of fulcra along the posterior margin of appendage E suggesting the transition from scales to fulcra; Figs. 15–16, faint impressions of flat dorsal surface of fulcra, Fig. 15 at the tip of the appendage, Fig. 16 about 16 mm. from the tip, R.E. 14783A; Figs. 17–19 show ventral surface with distinct fulcra and elongate scales, fig. 17 at the tip of the appendage, Fig. 18 about 18 mm. from the tip and Fig. 19 about 30 mm. from the tip, R.E. 14783B. $\times 6.7$.

PLATE VI

Figs. 1–2, *Adelophthalmus* (?) *perornatus* (Peach)

Fig. 1. Holotype, G.S.E. 2126, Glencartholm Volcanic Beds, River Esk, Glencartholm, Langholm, Dumfriesshire. $\times 0.7$.

Fig. 2. The same showing details of the ornament of the tergites. The scales become tongue-shaped towards the posterior margin of the tergites which is crenulate. $\times 2$.

Figs. 3–13, *Cyrtoctenus peachi* n. sp.

Fig. 3. Appendage B seen in ventral view, G.S.E. 12298, Cementstone Group, Longcraigs Bay, East of Belhaven Bay, Dunbar, East Lothian. $\times 0.7$.

Fig. 4. The same to show details of the fulcra at the posterior margin of the appendage at its distal end. $\times 7.4$.

Fig. 5. Details of the twisting of two filaments of appendage A, G.S.(L). R1729, Cementstone Group, Coomsdon Burn, Redesdale, Northumberland. $\times 11$.

Fig. 6. The ventral ornament of the rachis of the specimen shown in Fig. 3, exhibiting eurypterid type scales with seta sockets. $\times 7.4$.

Fig. 7. Detail of appendage A to show the development of flat spines along the convex anterior margin of the narrow rachis, G.S.E. 2183, Cementstone Group, Coldstream Bridge, Berwickshire. $\times 3.7$.

Fig. 8. Detail of appendage D showing three blunt spines at the anterior margin of the rachis. Holotype, G.S.E. 2184, Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 3.4$.

Fig. 9. Appendage D as in Fig. 8 to show fulcra and scales along the posterior margin. $\times 6.1$.

Fig. 10. Detail of appendage E showing distal fulcra nos. 3–6 from the tip of the appendage. A post-ventral view in which scales are visible at the bases of the fulcra, G.S.E. 9682, Cementstone Group, Lennel Braes, Tweedmill, Coldstream, Berwickshire. $\times 7$.

Fig. 11. The same. The left fulcrum (no. 3) extracted and seen in post-ventral view to show the sulcus. $\times 19$.

Fig. 12. The same in antero-ventral view showing teeth and slit along the anterior margin. $\times 19$.

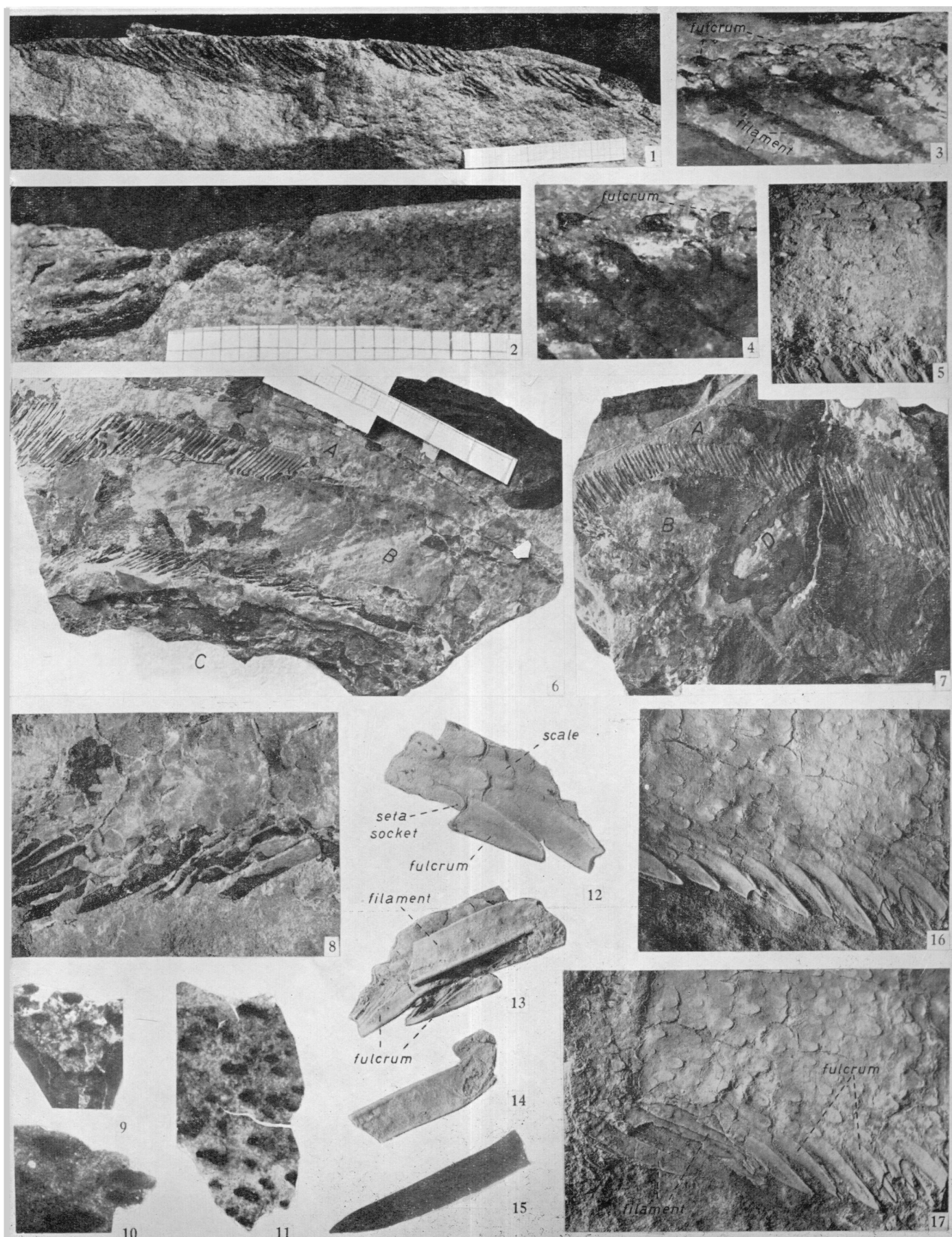
Fig. 13. The same, showing the tip of the appendage E in ventro-lateral view in which the distal parts of the fulcra are seen to be strongly bent in a dorsal direction. $\times 5$.

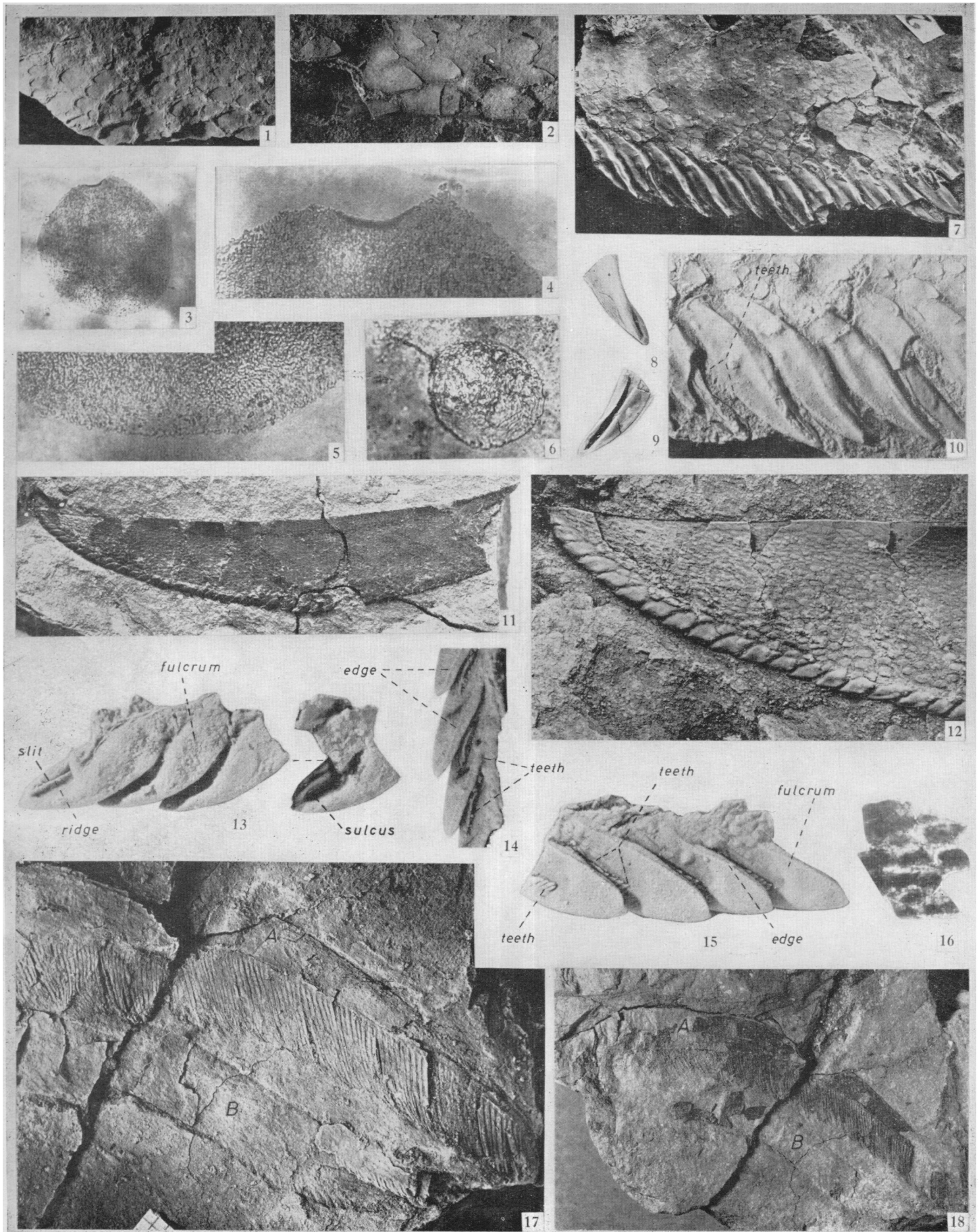
Figs. 14–15, *Cyrtoctenus dewalquei* (Fraipont) Assise d'Evieux, Pont-de-Bonne-Modave, Liège, Belgium.

Fig. 14. Fragment of appendage showing scales with seta sockets, R.E. 14786A. $\times 3.7$.

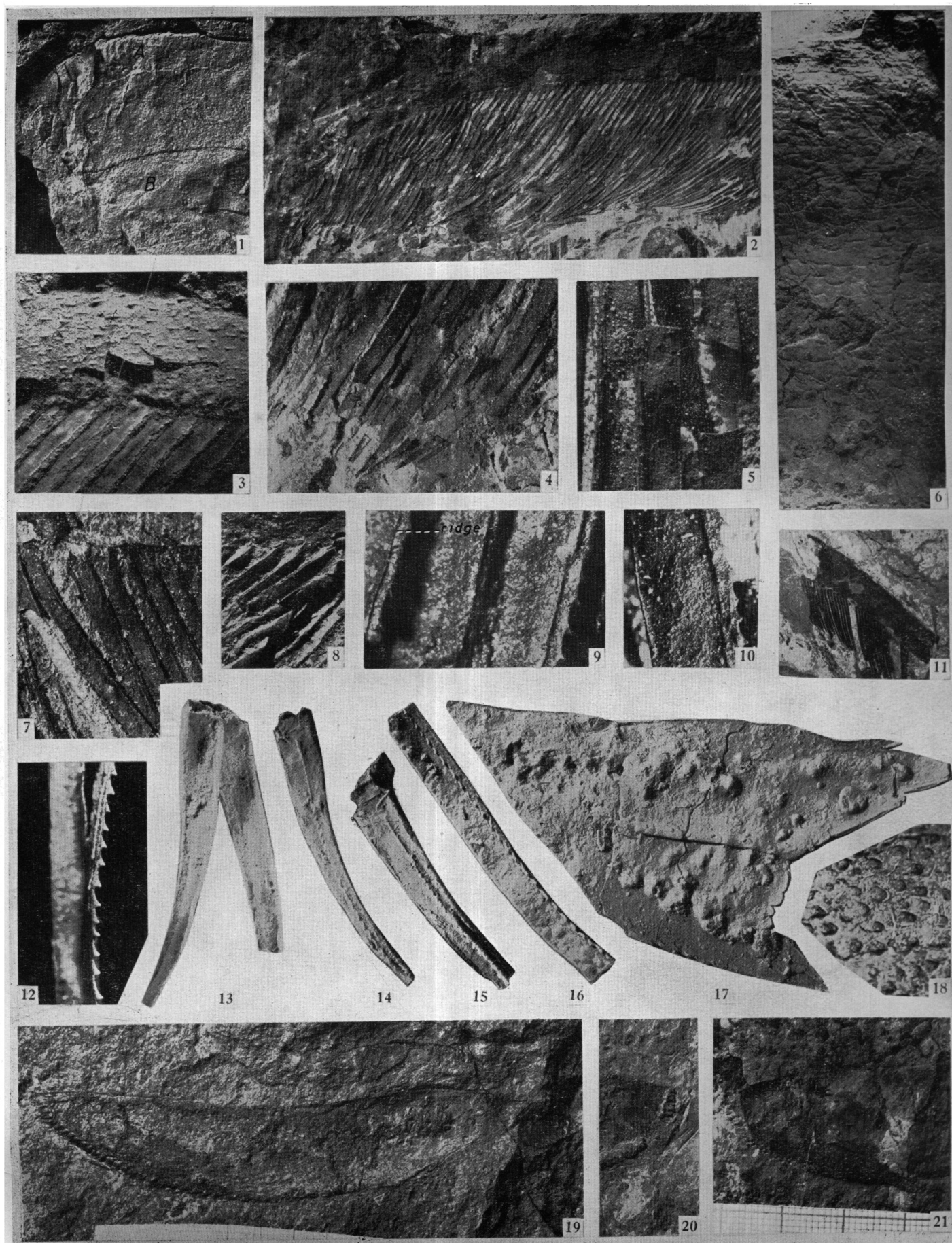
Fig. 15. Saprophytic (?) shells of "Spirula" on appendage E. Detail of specimen R.E. 14783A. $\times 3.1$ (cf. Pl. III, fig. 19).

LEIF STØRMER, D.Ph., and CHARLES D. WATERSTON, B.Sc., Ph.D., "*Cyrtoctenus* gen. nov., a large late Palaeozoic Arthropod with pectinate Appendages".—PLATE I.

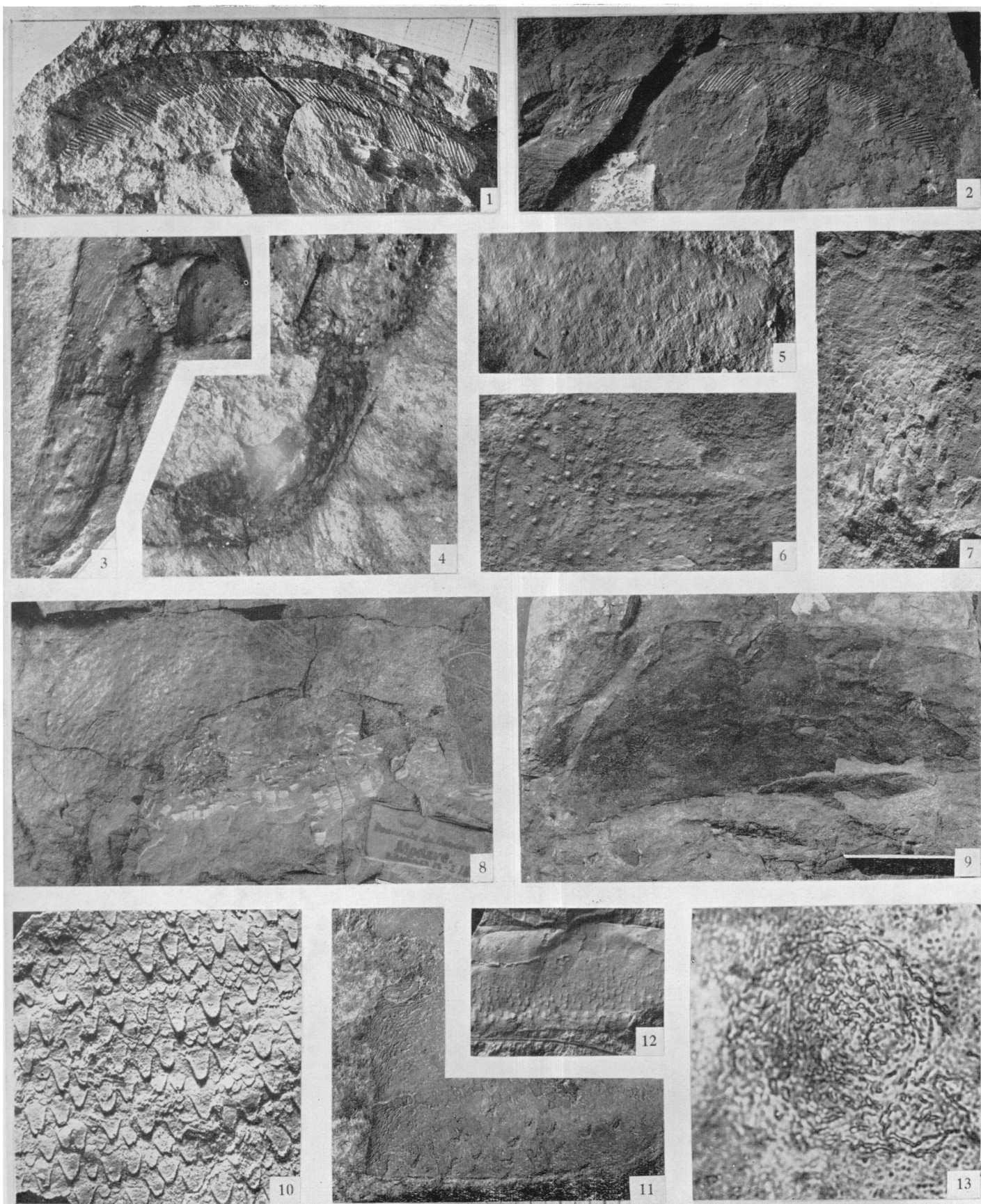




LEIF STØRMER, D.Ph., and CHARLES D. WATERSTON, B.Sc., Ph.D., "*Cyrtoctenus* gen. nov., a large late Palaeozoic Arthropod with pectinate Appendages".—PLATE III.



LEIF STØRMER, D.Ph., and CHARLES D. WATERSTON, B.Sc., Ph.D., "*Cyrtoctenus* gen. nov., a large late Palaeozoic Arthropod with pectinate Appendages".—PLATE IV.



LEIF STØRMER, D.Ph., and CHARLES D. WATERSTON, B.Sc., Ph.D., "*Cyrtoctenus* gen. nov., a large late Palaeozoic Arthropod with pectinate Appendages".—PLATE V.

